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A CONTRIBUTION TO THE KNOWLEDGE OF THE AMPHIPODOUS CRUSTACEAN, AMPITHOE VALIDA, SMITH 1873

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A CONTRIBUTION TO THE KNOWLEDGE OF THE AMPHIPODOUS CRUSTACEAN *AMPITHOE VALIDA* SMITH 1873

BY

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SECTION I

INTRODUCTION

General. The biology of any organism is complex and includes all aspects of the organism's environment, structure and function. It is inconceivable that one person, over a period of a lifetime, could discover and understand the complete biology of any one organism. Thus, it is realized that this is not to be considered the final word on the biology of the gammaridean amphipod, Ampithoe valida Smith.

It appears that man has a need to place everything he encounters, to some extent, into categories. At times he becomes confused in a mass of information and data. One consequence of this confusion is that the categories cease to be neat. Therefore, a discussion of the taxonomic status and the pertinent literature is included.

Any good study in biology involves explorations in varying degrees of depth into many fields. This is necessary if one is to inderstand the complex relationship of the organism as it now exists with its evolutionary history and environment. It is with this in mind, that many of these fields are investigated in this study. Because the morphology of most species is considered to be the most reliable and most widely

utilized method for determining the identity of the species (Mayr, Linsley, and Usinger, 1953), a discussion of the morphology with figures is presented.

Since reproduction and development are important phases in the life of any animal, they are considered. That these processes are necessary to the perpetuation of the species is a foregone conclusion. Thus, any information along these lines may possibly lead to knowledge concerning the systematic and ecological status of this species. With the same thought, a study of the habits and habitat of this species has been included.

As late as 1964, A. valida has been reported on the east coast of the United States only from its type locality (E. Mills, 1964). The species had also been recorded from the west coast of the United States by Alderman (1936) and Barnard (1954) and from Japan by Nagata (1960). The type locality is Beesley's Point, New Jersey. An extension of its known geographic range is included.

Taxonomy and Literature Survey. The species Ampithoe valida Smith was named in 1873 in the Report of U. S. Fisheries Commission For 1871-1872 by Verrill and Smith. The species was first mentioned by Verrill on page 315, where he stated:

> The second species, Amphithoe valida Smith is much smaller, being generally less than half an inch long. It is usually bright green in color and has black eyes. It often lives among the bright green fronds of Ulva latissima and its color is

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nearly that of the Ulva.

Not until page 563 did Smith describe the species. Smith's description covered only the antennae and the two pair of gnathopods for the male. With respect to the female, he only made slight mention of her differing from the male in regards to the gnathopods. Smith's description is quoted below:

> Male: Eyes round, black in alcoholic specimens. Antennulae and antennae subequal in length. Peduncle of the antennula extending scarcely beyond the distal extremity of the penultimate segment of the peduncle of the antenna; the second segment but little longer than the first; ultimate segment short and slender. Ultimate and penultimate segments of the peduncle of the antenna subequal in length. First pair of legs short, compressed; carpus as broad as the propodus; propodus broad, oval in outline, the posterior and palmar margins forming a continuous, nearly semicircular curve; dactylus fitting closely the palmary margin. Second pair of legs very large; carpus small; propodus oblong, broadest at the distal extremity, very large and thickened, the outer surface convex, the inner flattened, palmary margin transverse, with a broad, low median tooth, and a rounded prominance at the inferior angle, within which the tip of the very stout and strongly curved dactylus closes.
>
> The female differs in having the hands of the first pair of legs slightly more elongated and those of the second pair smaller than in the male, and the palmary margin slightly oblique.
>
> Color in life, bright green.
>
> Length, 10-13 mm
>
> New Jersey and Long island Sound.

Holmes (1905) placed the species in the synonomy of Ampithoe rubricata (Montagu) as did Kunkle (1918). It is suspected that in both of these works, the authors figured what appears to be an immature male of A. valida. Mills (1964) stated his suspicions along these lines but made no mention of the figures.

Stebbing (1906) included A. valida in his monograph of the gammaridean amphipods. In this work he described the species in very much the same manner as did Smith in his original description.

Because of the inadequacy of Smith's and Stebbing's descriptions Alderman (1936) elected to redescribe A. valida. Alderman described the male more thoroughly and included, besides the antennae and the gnathopods, the maxilliped, first and second maxillae, lower lip, first, second and third uropods and the telson.

Alderman did not figure the animal nor did he deposit specimens in any museum, nor did he describe an obvious female which he states he observed in copula with a male of the species.

J. L. Barnard (1954) included a discussion and figures for the male A. valida. He stated:

> Until comparison of Atlantic and Pacific material is made, this Pacific Coast identification must remain questionable.

Barnard examined specimens collected in Oregon. These specimens compare more favorably with the east coast specimens than do those of Alderman which were collected in California. Barnard's figures and discussion point out that the telson in Alderman's specimens is rounded and unlike those of the east coast specimens and those from Oregon.

Barnard (1954, 1958,1965) placed Ampithoe shimizuensis Stephensen in the synonomy of A. valida. Barnard (1965) now believes that there is justification to

give A. shimizuensis subspecific status. Nagle (unpublished) has taken A. shimizuensis from this synonomy entirely.

Eric Mills (1964) redescribed the male from Verrill's collection and appointed one lectotype, five adult males as paralectotypes and one juvenile paralectotype male. These type specimens were deposited in the Peabody Museum of Natural History at Yale University, (YPM 1230). Here again, the female of the species was not described other than to acknowledge that there was some confusion as to her identity. Smith's description of the female, as Mills points out, does fit that of an immature male.

Nagle (unpublished) described what he believed to be the female of A. valida Smith on the basis of three suppositions. These suppositions were as follows:

> Since (1) there were no other species of Ampithoe in the samples, (2) these females differed from the known ampithoids of the Cape Cod region, and (3) they exhibited two general characteristics diagnostic for the species (Mills, 1964), they were considered to be females of A. valida.

These suppositions leave doubt as to the validity of the description, especially since none of the described or studied specimens were deposited in any museum.

Generic and Family Considerations. The genus Ampithoe was erected in 1813 by Leach. The genus was included in the family Gammaridae at that time. The first mentioned species was Ampithoe rubricata (Montagu) (formerly known as Gammarus rubricatus). Since the establishment of the genus Ampithoe by Leach, the name of the genus has been variously misspelled and the genus has been placed in three

different families. In 1816, Latreille defined the genus as a group of crustaceans of the order Isopoda and began the long series of misspellings for the generic name by spelling it, Amphithoé. Since that time, the name of the genus has been spelled nine different ways. These spellings are Amphitoe, Ampithoe, Ampithoë, Amphithoe, Amphithoë, Amphitoé, Amphitoë, Amphithöe and Amphitöe. Stebbing (1888 and 1906) lists these spellings and their authors and dates. However, authors since that time have resorted to these various misspellings. Whiteaves (1901), Holmes (1901a, b and 1905), Kunkle (1910, 1918) and Schellenberg (1942) have spelled the genus Amphithoe. Skutch (1926), Stephensen (1944), Enquist (1949) and Bousefield (1956, 1958) have spelled the genus Amphithoë. Ruffo (1947) spelled the genus Amphithöe. With regards to the spelling of the genus, Stebbing (1888) stated:

> Since the very general acceptance of the form Amphithoë, I have considered that it would be inconvenient and pedantic to revert to the oddly spelt form Ampithöe, which Leach adopted at the first suggestion of the genus in 1813, and continued to use in his later writings.

It must be noted that in 1899 Stebbing then spelled the genus Amphithoe, and in his monograph in 1906 he reverts to the original spelling of Leach, but without the use of the diacritical marks. Since in Stebbing's own admission, Leach continued to use the name Ampithoe until 1818, it is felt by this author that this usage should be continued and that all other usages should be considered as incorrect spellings.

The family Ampithoidae was erected in 1899 by Stebbing. The erection of this family consisted of one sentence which is quoted below:

> Here it may be mentioned that I find it expedient definitely to establish the family Anamixidae, already suggested in 1897, and to institute various new families, namely:•••; Amphithoidae, for Amphithoe, Leach, and genera closely connected with it;•••.

Stebbing changed the spelling of the family name from Amphithoidae (1899) to Ampithoidae (1906) and since that time the majority of authors have continued to use Stebbing's spelling of the genus and family. It was not until 1906 that Stebbing gave a diagnosis for the family.

SECTION II

MARERIALS AND METHODS

Collecting and Collections. Monthly collections were made in the months of May through December, 1965. The times of day and month for the collections were as nearly the same as the weather and tides permitted. As many individuals were collected as were inhabiting ten quarts of drained Ulva. These collections were made from Great Bay, New Hampshire. Some living specimens were collected at Milford, Connecticut, and maintained for comparisons and crossbreeding.

Ampithoe valida were collected at four main localities within Great Bay. The collections consisted of Ulva taken intertidally by hand and subtidally with oyster tongs. The use of oyster tongs permitted subtidal sampling but did not ensure an accurate estimation of the numbers within the population. Usually many more empty tubes were found than were specimens. No quantitative data were taken as to the fluctuations within the populations. Relative numbers were kept for the adult males, adult females and immatures collected intertidally but are not considered significant for statistical analysis.

The procedure for collecting and isolating the individuals is simple and rapid. Once a bed of Ulva is located, a ten quart pail is filled with the alga. The

pail is then brought back to the laboratory where each blade and holdfast is inspected for the animal and its tube. Repeated inspections of the pail at the water-pail interface will reveal some individuals which have left their tubes.

A large number of individuals was collected from a cement block which was sunk to the bottom and marked by a buoy. The cement block had a thick mat of Ulva and approximately five millimeters of silt over the upper surface. The block had been submerged for three months.

Two other cement blocks were checked for this type of surface and were found to be barren. They did not appear to be in any beds of Ulva as was the first mentioned block. The greatest preponderance of animals was found after Ulva had been removed. They were living in tubes in the holdfasts and basal folds covered by the silt and mud. It is suspected that these tubes were built and then covered by silting rather than the amphipod burrowing into the silt and building the tube.

The success of locating A. valida in a known population is quite dependent upon obtaining the entire Ulva plant and its careful but rapid transfer to the collecting vessel. As will be discussed later in section V, the majority of the animals are found in the basal folds and not on the outer blade. Once located, the animals were placed into a series of culture dishes. Usually they were segregated into adult males, adult females and immatures.

Individuals to be preserved were subjected to a solution of chlorotone and sea-water. This anesthetized them within a few minutes, eliminating any autotomy which might occur if placed directly into ethanol.

The stock solution of chlorotone is saturated in sea-water at room temperature. The stock solution is then added to the culture water as needed. Usually an eyedropper full is sufficient for three to four ounces of culture water.

When collecting in areas where it is impossible to care for the animals as previously described, the entire collection may be placed in 95% ethanol and sorted out at a later date. The amphipods may be easily removed from the bottom of the container after a slight shaking to dislodge them. This is only a gross method and should be avoided because of autotomy.

Culture Methods. The study of habits, life cycles and tolerances, is facilitated by artificial culturing. This allows controlled experiments to be conducted which would otherwise be nearly impossible. In the culturing of A. valida, the temperature, salinity, food and shelter of the natural environment was approximated.

Culturing of this species is not difficult. Both adults and immatures can withstand a wide variation in temperature. The food used in the culturing during the spring, summer, and fall was Ulva. The technique described below was found quite satisfactory for the culturing of

both adults and immatures. Three inch finger bowls with straight sides were of sufficient size to contain enough of the culture water for a period of seven days without its becoming toxic to the individuals being cultured. The clear glass construction of the dish allowed light to enter from any angle. This facilitated photosynthesis by the Ulva in the dish.

The culture dishes were covered with plastic petri dish covers of appropriate size. The plastic covers tended to reduce evaporation and thereby maintain the culture water at constant salinity. Pertinent data were written on the plastic covers with a Dermatograph grease pencil. This combination of plastic cover and grease pencil proved to be quite useful as it did not matter if the cover was wet or dry. On glass, the grease pencil would write only on a clean and dry surface. As circumstances dictated, the grease pencil data could be removed quite easily with the use of a dry paper towel.

The culture medium used was full strength sea-water which was diluted with fresh-water to the desired salinity. When cultures were maintained at temperatures above 21°C, it was necessary to boil and filter the sea-water prior to its use. The addition of 25 mg. of Aureomycin powder to 1800 cc. of boiled filtered sea-water reduced the bacterial population and thereby indirectly the ciliate and flagellate contamination of the cultures. This measure was only necessary on occasions. The majority of the cultures were

maintained without the use of the Aureomycin.

The contaminating protozoa were identified by Dr. A. C. Borror as members of the flagellate genus Oxyrrhis and the ciliate genera Aspidisca, Diophrys and Lacrymaria. These organisms did not appear to be histophagic during the earlier stages of the population increase, but may have been the cause of mortality in the cultures after their population levels reached tremendous numbers. The mortality may have been caused by the bacteria which were indicated as being present by the increasing numbers of protozoa. The amphipods which did succumb in these contaminated dishes were completely covered by the ciliates and flagellates.

The numbers of amphipods maintained in the culture dishes ranged from one to three adults per dish to as many as sixty immature individuals per dish. As the immatures increased in size, they were separated into smaller groups. Growth proved to be inhibited and mortality increased by crowding. Ideally, one animal should be maintained per dish. However, this was not logistically possible. This was done for certain studies, such as moulting, but since the animal lives in competition, it was felt that this should not be the rule.

Cultures were maintained at temperatures of 12°C ±1°C and at room temperature. The room temperature varied daily but averaged 8°C higher than the temperature of the natural environment. Room temperature ranged from 20°C

to 31°C. The salinity in the culture dishes was maintained at $24^{o}/_{oo} \pm 1^{o}/_{oo}$. This salinity approximated that of the normal environment at low tide during the months of May through October.

A fluorescent lamp was used to maintain the illumination level above the compensation point for the Ulva (Figure II-1). It was found that the culture dishes with such illumination could be left unchanged for longer periods of time.

When the culture dishes and the medium were being changed, the old culture dishes were washed twice with cold fresh-water under pressure and then dried. They are then ready for the next change of dishes. Between the two washings, the dishes were scrubbed with a paper towel to dislodge any scum or foreign substances which was not removed by the water.

The culture water was changed every two days in those cultures which were maintained at temperatures above 20°C but below 27°C. In the cultures maintained at temperatures less than 20°C, the water was changed as appeared necessary as indicated by the condition of the Ulva and the relative degree of contamination by other organisms. In cultures maintained at temperatures over 27°C, it was necessary to change the water every day. In this case, it proved more useful not to use the Ulva as the source of food and shelter but to utilize Kimwipes as the source of shelter and to feed the animals daily with

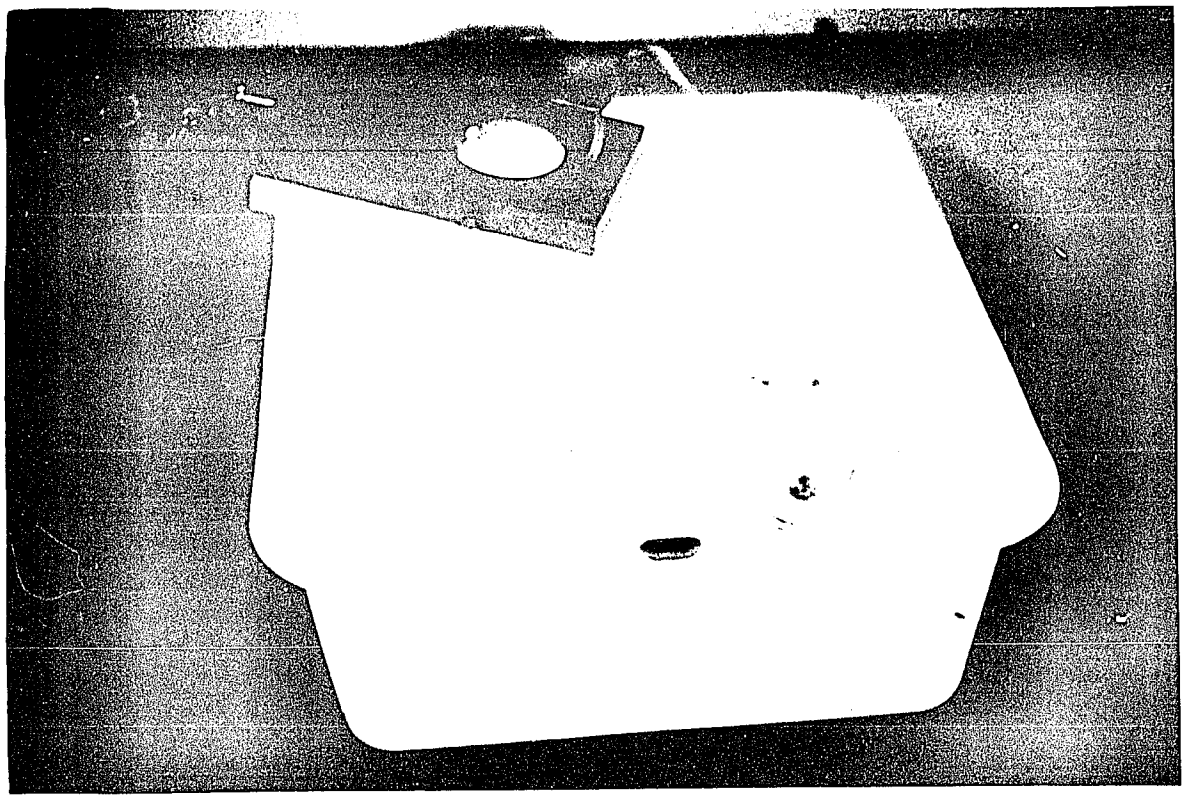

Figure II-1. Photograph of a culture tray showing the fluorescent lamp.

small portions of lettuce or Ulva. The use of lettuce facilitates the handling of the animal. The animal was very loath to stop feeding on the lettuce and could be manipulated during this time. The technique of using lettuce provided an easy method for observing the condition of the females with respect to the presence of eggs or immatures. It facilitated observation of the gnathopods in males and proved useful in the transfer of immatures from one dish to another.

The Ulva and lettuce used in the culture was washed in cold fresh-water and gently scrubbed. Ulva which had been washed and air-dried was found to be eaten by the animals in culture. This did not prove to be as effective in raising the animals as fresh Ulva or lettuce. If this dried Ulva is allowed to remain for any period of time over one day, the animals abstained from feeding and the Ulva turned completely bad.

Contrary to what was expected and that mentioned by Enequist (1949), no problems were encountered with regards the animals becoming bound in the surface film. At times the immatures would have some small air bubbles attached to them but these were usually of no consequence to them. It was observed that if an adult did become bound by the surface film, it would rapidly flex its body backwards and then with a burst of speed, rapidly swim down to the bottom. If the first attempts were not successful, one or more attempts of this manner would be tried until it was successful. Never

was it observed to be unsuccessful.

Measurements and Statistical Analysis. Body length was determined by measuring the entire length of the individual from the anterior tip of the rostral region to the posterior tip of the telson. Since the animal may assume a number of positions, which ultimately affect the final measurement, each segment was measured with a calibrated ocular micrometer. The sum total of all the lengths resulted in the total body length. This method of measurement closely parallels that used by Clemens (1950). This method is considered to be more accurate and reliable than other techniques employed.

In measuring the various parts and regions of the female, 128 different morphometric measurements were taken. The areas measured were:

Total body length
Eye length and width
Interantennal lobe length and width
Mandibular palp segments 1, 2 and 3 for length and width
Antenna I peduncular segments 1, 2 and 3 length; flagellum length
Antenna II peduncular segments 1, 2, 3, 4 and 5 length; flagellum length
Maxillae I palp segment one for length and two for length and width
Maxilliped palp segments 1, 2 and 3 for length and width
Gnathopod I dactyl and palm length; length and width of propodus, carpus, merus, ischium, basis and coxal plate
Gnathopod II dactyl and palm length; length and width of propodus, carpus, merus, ischium, basis and coxal plate
Pereiopods I, II, III, IV and V length and width of propodus, carpus, merus, ischium, basis and coxal plate
Uropods I, II and III length of basis, endopodite and exopodite
Telson length and width

Measurements taken for the determination of growth in the first six moults were taken on the exuvia. The areas measured in these individuals were as follows:

Length of Antenna I flagellum and peduncular segments 1, 2 and 3
Length of Antenna II flagellum and peduncular segments 3 and 4
Length of cephalon
Total body length
Length of the basis, endopodite and exopodite for uropods I, II and III

The exuvium was chosen for measurement because it represented the maximum growth during the intermoult and was more easily measured than the live animal. It also facilitated the measurement at convenient times.

In general, the measurements were taken for the maximum length and width attainable. Length in appendages was determined as the distance between the most proximal end and the most distal end (Figure II-2). In cases where terminal claws or spines are present, they are not included as part of the measurement. Width was determined to be the widest measurement attainable on an axis perpendicular to the length axis (Figure II-2). In measuring the length of the eye and interantennal lobe, the length was determined as that distance measured on the antero-posterior axis. The width was taken at right angles to the length (Figure II-2).

All measurements were taken with the use of a Bausch and Lomb stereoscopic zoom dissecting microscope, model number BVB-73 and a Bausch and Lomb Dynazoom compound microscope, model number PG-42. The range of magnification used on the stereoscopic scope was 20X to 30X.

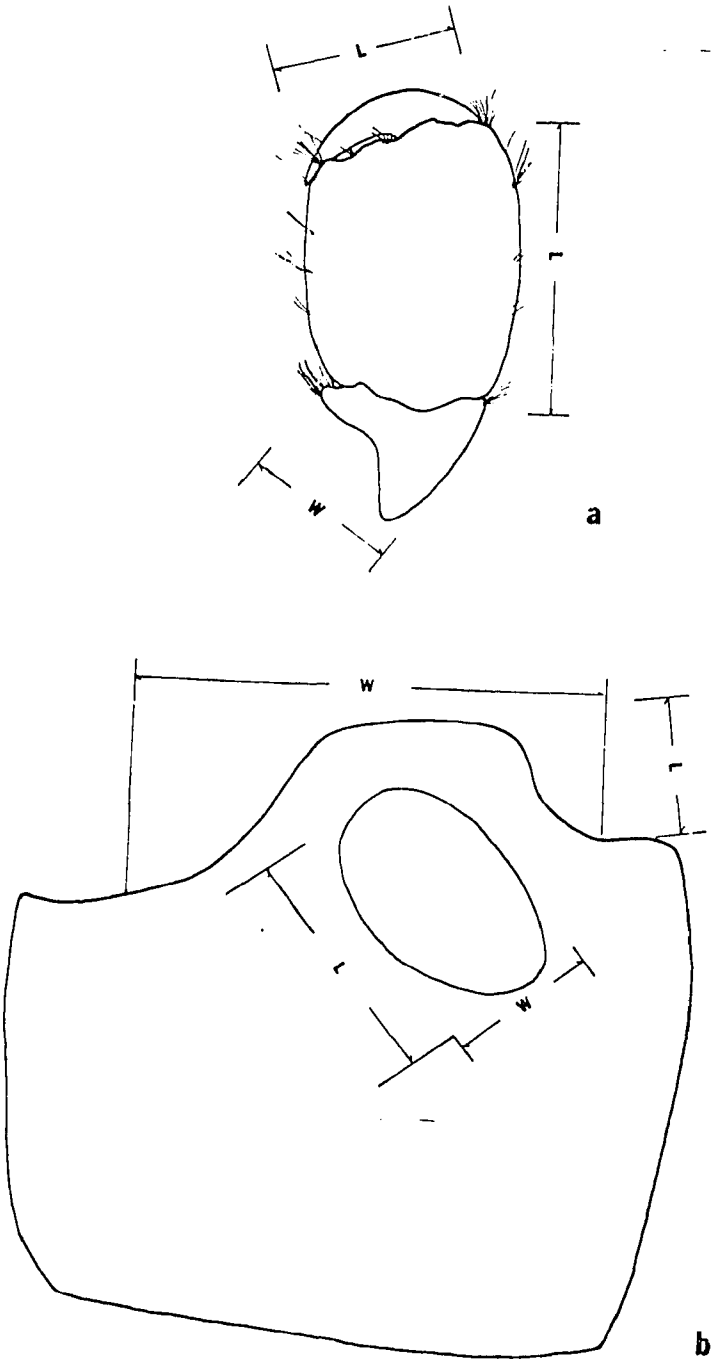

Figure II-2. Examples of methods of measurements.

a. Second gnathopod.

b. Cephalon with interantennal lobe and the eye.

The range of magnification used on the Dynazoom microscope was 17X to 50X.

Once all the measurements were taken, the data were arranged in reference to either the total body length or the intermoult period. One millimeter size classes were segregated and treated separately. A size class was determined as ranging from the extremes of the whole numbe. (i.e. 11.0 millimeters to 11.9 millimeters equals the 11 millimeter size class). A tabulation of the mean values for each area measured by size class is given in Appendix A. All linear measurements were compared on a percent ratio basis rather than the actual linear length in millimeters (Appendix B). This method shows any heterogonic growth between size classes and gives an indication of those areas which have little or no variation during growth and aging. This method also indicates the relationship between certain morphological regions. Appendix C contains mean armament counts by size class. The mean value was utilized in the determination of the percent ratios.

Statistical analysis of the data and plotted graphs was carried out with the aid of Croxton's text (1953). Regression coefficients were determined by the method of least squares. Coefficients of correlation "r" for these plotted functions were calculated and a "P" value was determined. When it was necessary to explain any ambiguity between "r" and the resulting "P" values, the coefficient of determination was included.

Line drawings of the morphology of the egg and female were drawn from projected images with the use of a Bausch and Lomb Microprojector, Type 42-53-59. With the exception of the egg, the parts were dissected from the animal, dehydrated in absolute alcohol and cleared in toluene prior to projection and drawing.

Difficulty was encountered at times in determining the exact spination of the uropods. The problem occurred in individuals which were near the end of the intermoult period. The new spines would be retracted from the old spines and thereby gave the appearance of more spines present than there actually were. Once this was realized, the counting and locating of these spines was more accurate and simple.

Mileage involved in the extension of the known geographic range was determined as the distance along a longitudinal meridian beginning at the latitude of the southern tip of Long Island Sound and also Barnstable Harbor and ending at the latitude of the population area studied.

SECTION III

MORPHOLOGY

The description of the male of A. valida has been done with a fair amount of accuracy. In addition to Mill's (1964) description, there are some features and ranges which I believe should be added. This section will, however, be primarily concerned with the description of the female of the species and a comparison of the east and west coast populations.

Male. The eye is ovoid in shape, having a length to width ratio of 1/.75. This ratio is a mean value, as are all such ratios used in this section, determined from a series of means for seven size classes. The color in life is black with some white pigmentation.

The interantennal lobe has an anterior-posterior length to dorsal-ventral width ratio of 1/2.74.

Incisor teeth of the mandible are seven in number in most cases. There are three large teeth and four smaller teeth present. The small teeth are of such a nature that they may be miscounted.

The spination of the second segment of the first maxilla palp ranges from five to eight stout spines. The setation on the external side of this segment ranges from one to three setae.

The flagellum of the first antennae of the

population utilized in this study never attained 35 articles. The range for adult males was 23 to 30. The second antennae are not always subequal to the first antennae but may be equal to or slightly longer than the first. The range of flagellar articles in the second antennae was 15 to 20.

Pereiopods I and II with the propodus equal in length to the carpus and narrow. The length to width ratios of the propodus and carpus are 1/.26 for the propodus of pereiopod I, 1/.27 for the propodus of pereiopod II; 1/.27 for the carpus of pereiopod I and 1/.34 for the carpus of pereiopod II. Merus inflated along the anterior margin. Resulting configuration a very characteristic convex curvature. Antero-distal region of the merus projecting over the carpus.

Pereiopod V basis bears a small spinule on the postero-distal angle.

Uropod I peduncle bears four to seven spines along the external border and four to seven spines along the medial border. Exopodite bears three to six spines along the external lateral border and is spineless along the medial border. Endopodite bears two to four spines along the medial border. It has no spines along the external lateral border. Uropod II peduncle bears two to four spines along the medial border and two to four spines along the lateral border. Exopodite bears two to five spines along the lateral border and is apparently spineless along the medial border. Endopodite bears two or three spines along the medial border

and again no spines have been observed along the lateral border. Uropod III peduncle bears two to four postero-dorsal spines at the base of the exopodite, two spines along the lateral border and one spine on the postero-dorsal medial border.

Female. (Figure III-1, 2, 3, 4, 5, Appendices A, B-1, 2 and C). Rostrum lacking. Eyes oval in shape with a length to width ratio of 1/.76. Black in life with some white pigmentation present in the larger females.

Interantennal lobe quadrate with the corners rounded. Length to width ratio of this lobe being 1/3.06.

First Antennae (Figure III-3,a). First peduncular segment heavier than the second or third. First peduncular segment usually with one to three tufts of setae along the ventral borders. Second peduncular segment subequal to the first and much slimmer. Second peduncular segment bears one to four tufts of setae along the ventral border. Third peduncular segment smallest and approximately one third the length of the first. Flagellum averages 3.70 millimeters in length, ranging from 2.35 millimeters for the eight millimeter size class to 4.65 millimeters for the 14 millimeter size class female. The number of articles in flagellum averages 24, ranging from 18 to 28 for the same size classes as mentioned previously. The ratio of the lengths of the first peduncular segment to the second peduncular segment, third peduncular segment and flagellum is 1/.90/.36/5.02.

Second Antennae (Figure III-4,a). Shorter than the first antennae. Fifth peduncular segment shorter than the fourth. Total length of the flagellum slightly more than the combined lengths of the fourth and fifth peduncular segments. Ratio of the length of the fourth peduncular segment to the fifth peduncular segment and the flagellum is 1/.92/2.27. Ratio of the fourth plus the fifth segment lengths to the flagellum length is 1/1.18.

Mandible (Figure III-2,b). Incisor with seven sharp teeth. Three large teeth and four small teeth. Lacina mobilis dentate. Four to six stout setae arranged between the incisor and the molar process. Molar process with fine serrations along the posterior edge. Palp three segmented with the third segment slightly expanded, flattened and angular, bearing a row of setae which become progressively shorter towards the base along the anterior edge. Palp setae do not progress beyond the defining angle and are the only setae on the segment. Length to width ratio of this segment is 1/.38.

Maxilla I (Figure III-2,d). Medial plate unarmed. Lateral plate with ten stout curved spines. Palp two segmented, the distal segment bearing five to eight spines. The setation on the external side of the second segment ranges from two to four setae. The length to width ratio of the second segment averages 1/.34.

Maxilla II (Figure III-2,e). Medial lobe narrower than the lateral lobe and subequal to it in length. Both

lobes with setae along their inner borders leading to a dense tuft of setae at the apices. Medial lobe more densely setose than the lateral lobe.

Maxilliped (Figure III-2,f). Medial lobe reaching to and just beyond the base of the lateral lobes. Medial border of the medial lobes densely fringed with short setae. Apices densely setose with longer setae than those of the medial borders. Lateral lobes large and extending beyond the second segment of the palp. Medial borders armed with short spines which become longer as the apices are reached and passed laterally. Palp four segmented and terminating in a claw. Basal segment with a lateral projection reaching from one third to one half the length of the second segment. Second segment longer than any of the other segments. Third segment nearly circular in shape. Fourth segment conical in shape.

Gnathopod I (Figure III-3,b). Coxal plate produced anteriorly and somewhat deeper then wide. Postero-distal border bearing one to four setae. Length to width ratio being 1/.88. Basis with an antero-distal lobe bearing one or two small setules. One proximal tuft of long setae posteriorly. Merus projecting somewhat distally in large females. Carpus nearly equal to propodus in length and equal to or larger than propodus in width. Carpus projected posteriorly to a broad lobe bordered by a series of tufts of setae. Propodus moderate, palm oblique and slightly convex with the palmar angel defined by a spine. Two to

five tufts of setae border the anterior edge of the propodus. The palm is densely setose with small tufts of short setae interspersed with longer setae. Dactyl stout and curved, fitting the convex palm. Dactyl slightly longer than the palm. Dactyl length to palm length ratio is 1/.93. Propodus length to carpal and meral length ratio is 1/.81/.52. Length to width ratio of the propodus is 1/.51. The length to width ratio of the carpus is 1/.62.

Gnathopod II (Figure III-3,c). Coxal plate rectangular in shape. Antero-distal angle rounded. Length to width ratio is 1/.70. Postero-distal angle bears two to five setae, the posterior-most one being the longest and the remainder gradually decreasing in length toward the anterior-most one. Basis with a broad antero-distal lobe bearing one to two setules. Postero-proximal border bearing one tuft of moderately long setae. Merus produced distally and bearing one dense tuft of setae along the distal border. Carpus essentially triangular in shape and produced between the merus and propodus. Length very slightly longer than the width. Produced angle bearing a large dense tuft of setae. Propodus larger than that of gnathopod I but similar in shape. Palm oblique with a spine defining the palmar angle. Dactyl stout and only slightly longer than the palm. Dactyl length to palm length ratio is 1/.94. Propodus length ratio to the carpal and meral length is 1/.59/.60. Length to width ratio of the propodus is 1/.59. Length to width ratio of the carpus is 1/.97.

Pereiopod I (Figure III-3,d). Coxal plate rectangular with the anterior corner rounded. Length to width ratio is 1/.70. Postero-distal angle armed with three to six long setae. Posterior most seta longest. Basis somewhat expanded and ovoid in shape bearing one to three setules on the antero-distal border. Merus broadly inflated anteriorly. Anterior border convex and produced antero-distally over the carpus. Bearing one to three tufts of setae along the posterior border. Carpus long and narrow bearing three to six tufts of setae along the posterior border. Propodus very slightly longer than the carpus and narrower than the carpus bearing two to four tufts of setae along the posterior border. Length to width ratio of the propodus, carpus and merus are 1/.26, 1/.34 and 1/.54 respectively. Ratio of the length of the propodus to the carpal and meral lengths is 1/.98/.96.

Pereiopod II (Figure III-3,e). Coxal plate similar in shape to the coxal plate of pereiopod I but larger. Distal border bearing three to six small setules somewhat anteriorly and a group of four to six long setae posteriorly. Basis slightly more expanded than in pereiopod I. Merus similar in shape to that of pereiopod I. Length to width ratio being 1/.57. Carpus and propodus similar to those of pereiopod I. Length to width ratios being 1/.35 and 1/.27 respectively. Length to length ratio of the propodus to the carpus and merus is 1/.98/.95.

Pereiopod III (Figure III-4,b). Coxal plate broad with a hind lobe. Total width of plate and hind lobe equal

to the length. The ratio being 1/.99. Length to minimum width (without hind lobe) being 1/.78. Basis nearly circular in shape. Anterior border armed with small spines. Length to width ratio is 1/.96 with a range of 1/.91 to 1/1.00. Carpal segment approximately one half as wide as long. Ratio 1/.56. Propodus longer than the carpus and only slightly longer than the merus, armed with two to five spines.

Pereiopod IV (Figure III-4,c). Shorter than pereiopod V. Coxal plate bilobed, anterior lobe the largest. Maximum length to width ratio being 1/.52. Basis expanded to an oval shape. Length to width ratio is 1/.66. Armed anteriorly with two to four small spines. Postero-distal angle bearing a small spinule. Propodus elongated and armed with four to six spines. Each spine accompanied by a seta. Length to width ratio of the propodus is 1/.24. Length to length ratio of the propodus to the carpus and merus is 1/.71/.92.

Pereiopod V (Figure III-4,d). Coxal plate shallow, unarmed, somewhat rectangular and slightly broader anteriorly. Length to width ratio is 1/.59. Basis more elongate than basis of pereiopod IV. Armed with two to five spines anteriorly and seven to ten small setules posteriorly. Postero-distal angle bearing a small spinule. Length to width ratio of basis is 1/.59. Propodus elongate and armed anteriorly with four to six spines. Each spine accompanied by one or two setae. Length to length ratio of propodus to carpus and merus is 1/.72/.92.

Uropods (Figure III-5 a,b,c). Uropods all reaching equally distant posteriorly. Uropod I peduncle longer than either ramus. Length to length ratio of the peduncle to the exopodite and endopodite is 1/.58/.63. Peduncle armed with five to seven spines on the external lateral border and four to six spines on the medial border. Exopodite shorter than the endopodite and armed on the external lateral border with four to eight spines. Terminal spine relatively short and accompanied by two accessory spines. Endopodite armed on the medial border with two to five spines. Terminal spine accompanied by two accessory spines. Uropod II peduncle longer than either ramus. Length to length ratio of the peduncle to the exopodite and endopodite is 1/.63/.76. peduncle armed with two to four spines on both the external lateral and medial borders. Exopodite shorter than the endopodite, armed on the external lateral border with two to five spines. Unarmed on the medial border. Terminal spine short and accompanied by one or two accessory spines. Endopodite armed on the medial border with two to four spines. External lateral border usually unarmed but occasionaly one to two spines may be present (Figure III-5b). Uropod III peduncle equal to or greater than twice as long as either ramus. Length to length ratio of the peduncle to the exopodite and endopodite is 1/.43/.50. Peduncle armed postero-dorsally with two to four spines at the base of the exopodite, with one to two on the external lateral border and one spine on the medial dorsal posterior

corner. Bearing one to four tufts of long setae on the medial ventral border. Exopodite bearing two strong recurved hooks, the anterior hook being somewhat shorter and stouter than the posterior hook. Several long setae on the external lateral border. Endopodite with four to six spines apically and accompanied by six to fifteen stout setae. One spine located on the external lateral border two thirds the distance from the base.

Telson (Figure III-5,d). Broader than long bearing one to four setae along the lateral borders and a pair of long stout setae on the posterior border. Posterior angles lobed and bearing a setule in the medial corners of the lobe.

Immature. Immature males resemble adult and immature females until they have attained a length of four to five millimeters. At this point they begin to show the medial palmar tooth and develope the copulatory organs. Immatures of A. valida may be recognized by the relative length to width ratios of the propodus, carpus and merus of the pereiopods I and II and by the length to length ratios of these same three segments. The mandibular palp is characteristic for the species and is useful in determining the identity.

Immatures of this species are most easily confused with those of A. longimana. However, the mandibular palp will differentiate them.

Most immatures and young adults show an indentation on the posterior edge of the basis of pereiopods I and II.

This indentation may be continued to the anterior border, thus causing a constriction. The indentation is at the site of a tuft of setae.

Discussion. In the collection catalogued YPM 1230 held at the Peabody Museum of Natural History, Yale University, there are specimens of both sexes which are not A. valida. These specimens are believed to be immature males and mature females of A. longimana. Mills (1964) pointed out that Verrill and Smith's original collection contained both species. In working over the specimens labeled as paralectotype immature females, it was found that none of these specimens belonged to the species A. valida. In the vial labeled as paralectotype males, three specimens were found to be A. valida.

Ampithoe valida is easily distinguished from the two closest species found on the east coast of the United States, A. rubricata and A. longimana (Figures III-6, 7, 8). The adult male is distinguished by the characteristic second gnathopod, mandibular palp and the shape of the propodal, carpal and meral segments of the first two pairs of pereiopods. The immature and adult female may be distinguished on the basis of: the relative lengths of the fourth and fifth peduncular segments of the second antennae; the length of the flagellum of the second antenna as compared to the fourth and fifth peduncular segments; the shape and setation of the third segment of the mandibular palp; shape of the basal segment of the maxillipedal palp; relative length ratio

of the dactyl to palm; relative length to width ratio of propodus to carpus and merus of pereiopods I and II; shape of the meral segment of pereiopods I and II; the condition of the postero-distal angle of the basis of the fifth pereiopod and the armament of the uropods.

Nagle's (unpublished) description of the female agrees in some points but differences which have been noted in this study will be mentioned. Nagle stated that the first and second peduncular segments of the first antennae are equal. In measuring better than one hundred females, the ratio has been found to be 1/.90 for all size classes. The range for this mean value is from 1/.84 to 1/.94. Measurements taken on females collected in Milford Harbor in Long Island Sound agreed with those from Great Bay. Nagle mentions that the coxal plate of pereiopod II is excavate behind. This does not agree with the specimens from Great Bay or Long Island Sound. His description of the coxal plate of pereiopod IV is that it is suboval when in actuality it is bilobed. He stated that the postero-distal angle of the basis of pereiopod V has no spine or spinule but indicates in his figure 2 C-3, a brush of short setae in this region. My observations have never shown me this brush of setae. In 97 per cent of females examined, a spinule was present on the angle. His statement of color for this species can be broadened to include brown, dark green and almost black. The length of nine to ten millimeters is in the middle of the range for the adult female A. valida.

Specimens have been collected which have attained a length of 16 millimeters and have been raised in culture to a maximum length of 18.5 millimeters.

In agreement with Nagle, I believe that Ampithoe shimizuensis should be taken from the synonomy of A. valida. This belief is based only on Stephensen's description and text figures. A. shimizuensis differs primarily in the propodus of the first gnathopod for both sexes, armament of the peduncle of uropod I, fourth peduncular segment of the second antennae and the round shape of the telson. Barnard (1965) believes that A. shimizuensis should be given subspecific status. If Stephensen's figures are accurate and do represent the population, then I believe specific status is necessary and it certainly should not be combined with A. valida. Nagata (1960) in accordance with Barnard's earlier works (Barnard, 1954, 1958) has placed A. shimizuensis in the synonomy of A. valida. He has figured the first and second gnathopods of a female which he has called A. valida. These two figures do agree favorably with that of a female A. valida and not with those of A. shimizuensis. However, many of the females in this genus have gnathopods which are nearly identical. Nagata believes that his specimens agree favorably with those of Barnard and on the basis of this, it would be possible to conclude that Nagata was working with A. valida and not A. shimizuensis.

West Coast Specimens. Ten specimens of the west coast population were examined and compared with the east

coast specimens. In general, they compared favorably. There were some dissimilarities noted. The following comparisons are based on seven females.

The eyes of the west coast specimens tended to be somewhat more elongate, averaging 1/.65. The interantennal lobe is less prominent. Length to width ratio being 1/3.50 as compared to 1/3.06.

The ratio of the first peduncular segment of the first antennae to the second peduncular segment averaged 1/.94 for the west coast specimens as compared to 1/.90 for the east coast specimens. The ratio of the first to third peduncular segments for both populations are the same.

The length to length relationship of the fourth peduncular segment of the second antennae to the flagellum is lower for the west coast specimens. The mean ratio is 1/1.86 as compared to 1/2.27. Likewise the length to length ratio of the fourth and fifth peduncular segments to the flagellum shows the flagellum to be shorter than their combined lengths. This ratio is 1/.98 as compared to 1/1.18 for east coast specimens.

The gnathopods of the west coast specimens differ the most in morphometry. The carpal segment of the first gnathopod is wider in relation to its length than is the same segment of the east coast specimens. The ratio is 1/.66 as compared to 1/.61. The 1/.66 does not fall within the ranges for the east coast specimens. The merus of the first gnathopod of the west coast specimens is longer with

respect to the propodus than is found in the east coast specimens (1/.59 versus 1/.54) and does not fall within the ranges for the east coast specimens. The dactyl to palm length ratio is greater for the west coast specimens. This ratio is 1/.98 as compared to 1/.93 and does not lie within the ranges. In gnathopod II, the propodus is slightly broader in relation to length than is found for east coast specimens and the carpus is narrower. The ratios being 1/.62 versus 1/.59 for the propodus and 1/.94 versus 1/.97 for the carpus. The ratios for the west coast specimens do lie within the ranges of the east coast specimens. However, the length to length ratio of the propodus to the carpus and merus does not. This ratio is 1/.66/.65 as compared to 1/.59/.60.

The shape of the first and second pereiopods are very similar with the only notable difference being in the relative widths of the propodus, carpus and merus. The west coast specimens have a higher length to width ratio than do the east coast specimens. All, except for the length to width ratio of the propodus of pereiopod II, lie within the ranges found for the east coast specimens.

The one adult male included in the collection sent from the Allan Hancock Foundation appears to be a very aberrant specimen of this species or one of a different species that is superficially similar.

Barnard's (1965) figure of a male A. valida agrees in most respects with the east coast specimens. There are some differences which involve the pleonal hook, coxal

plate of gnathopods I and II, setation of the propodus of gnathopod I and the coxal plate of pereiopod IV.

In all other aspects, the west coast specimens appeared to be morphologically similar to the east coast specimens. As to whether or not these two populations are the same species, more specimens of a wider range of sizes should be examined and if possible, culturing and cross-breeding studies should be undertaken. At the present time, this is not possible. I do not believe that they should be split. I do believe that the differences noted could well be within the normal for the species and are nothing more than ecophenic expressions.

Figure III-1. Adult female Ampithoe valida Smith

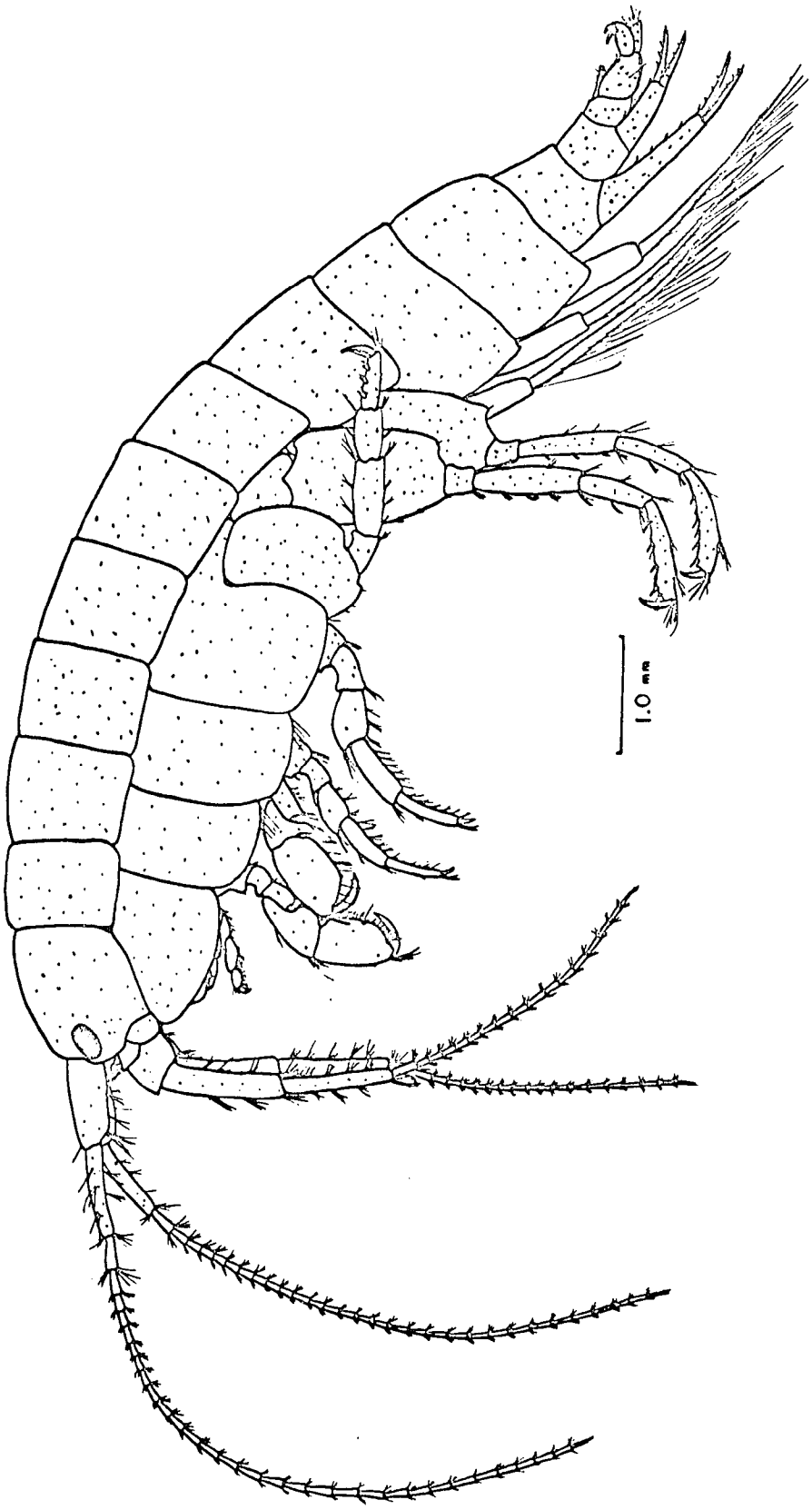

Figure III-1

Figure III-2. Mouthparts of adult female A. valida

a. Upper lip

b. Mandible

c. Lower lip

d. Maxilla I

e. Maxilla II

f. Maxillipeds

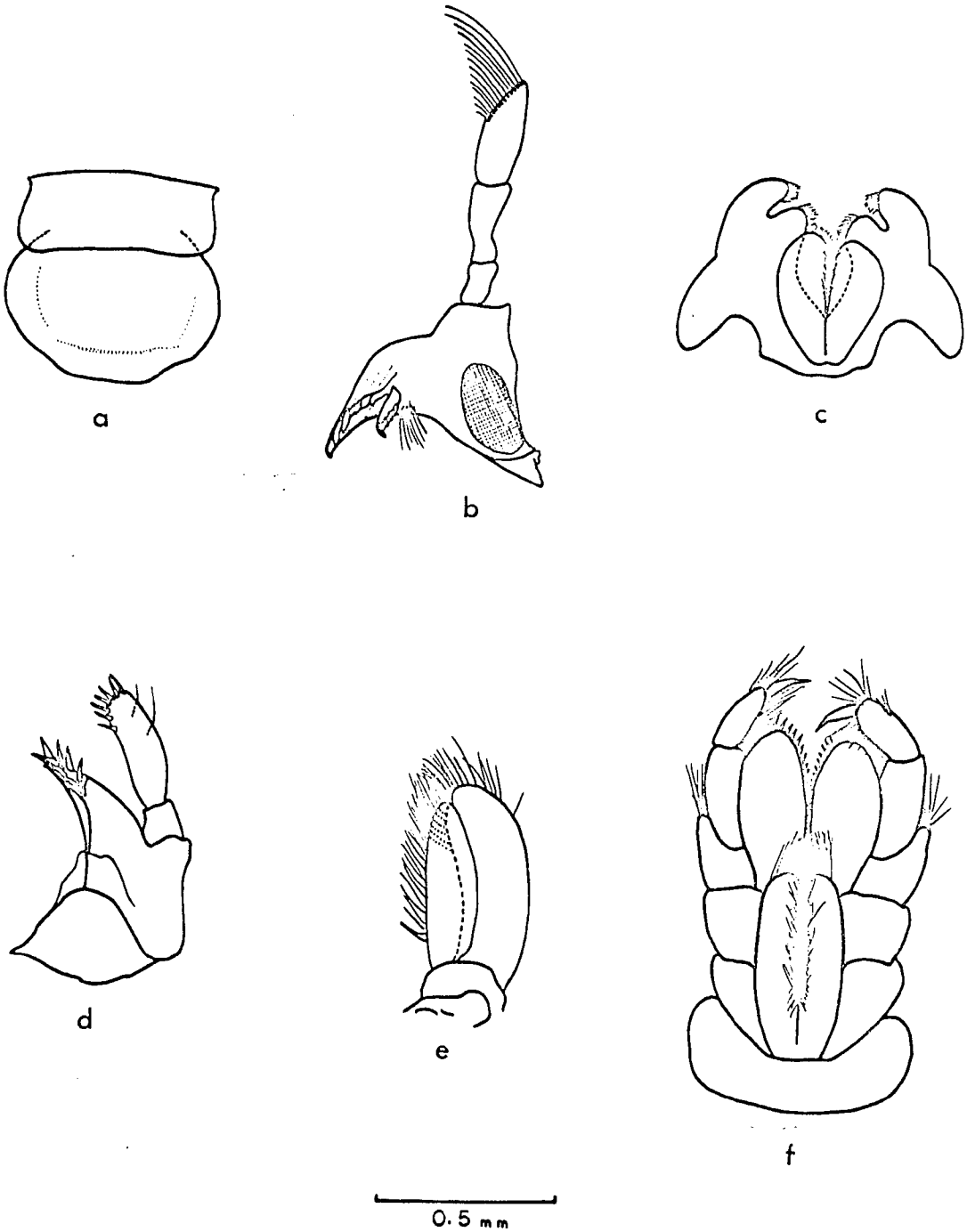

Figure III-2

Figure III-3. Appendages of adult female A. valida.

a. Antenna I (flagellum incomplete)

b. Gnathopod I

c. Gnathopod II

d. Pereiopod I

e. Pereiopod II

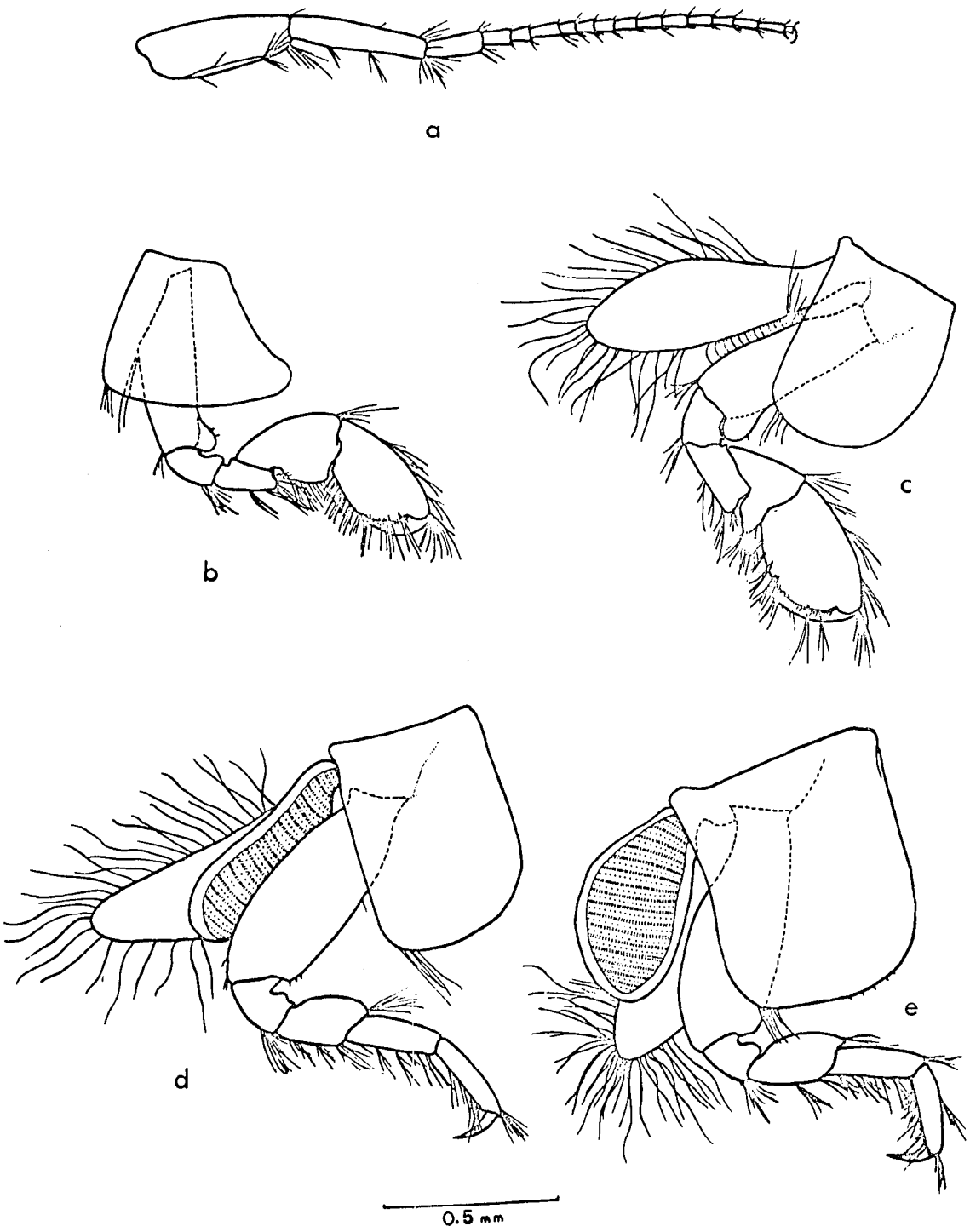

Figure III-3

Figure III-4. Appendages of adult female A. valida.

a. Antenna II (flagellum incomplete)

b. Pereiopod III

c. Pereiopod IV

d. Pereiopod V

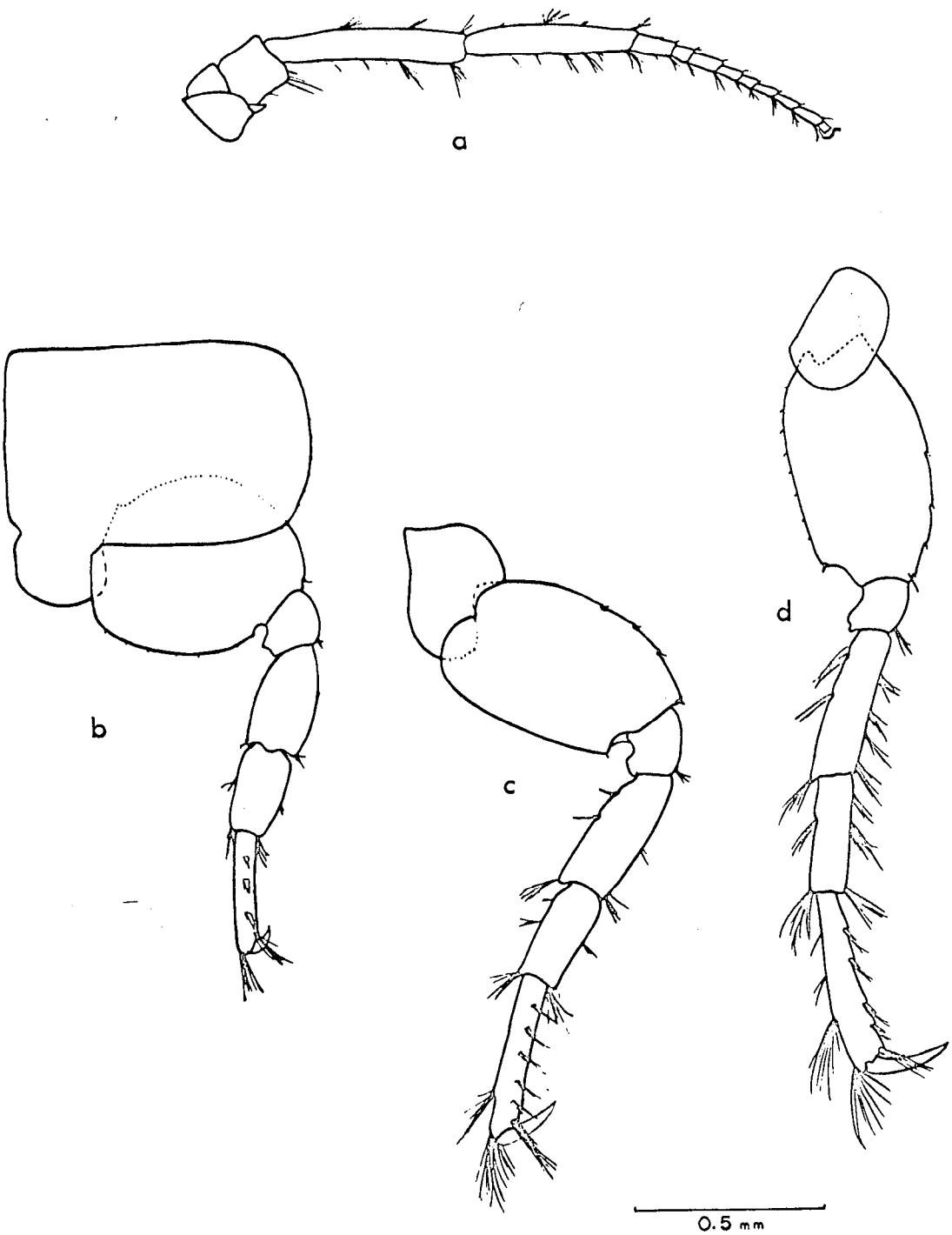

Figure III-4

Figure III-5. Urosomal appendages and telson of adult female A. valida.

a. Uropod I

b. Uropod II. Showing the unusual pair of spines along the lateral border of the endopodite.

c. Uropod III

d. Telson

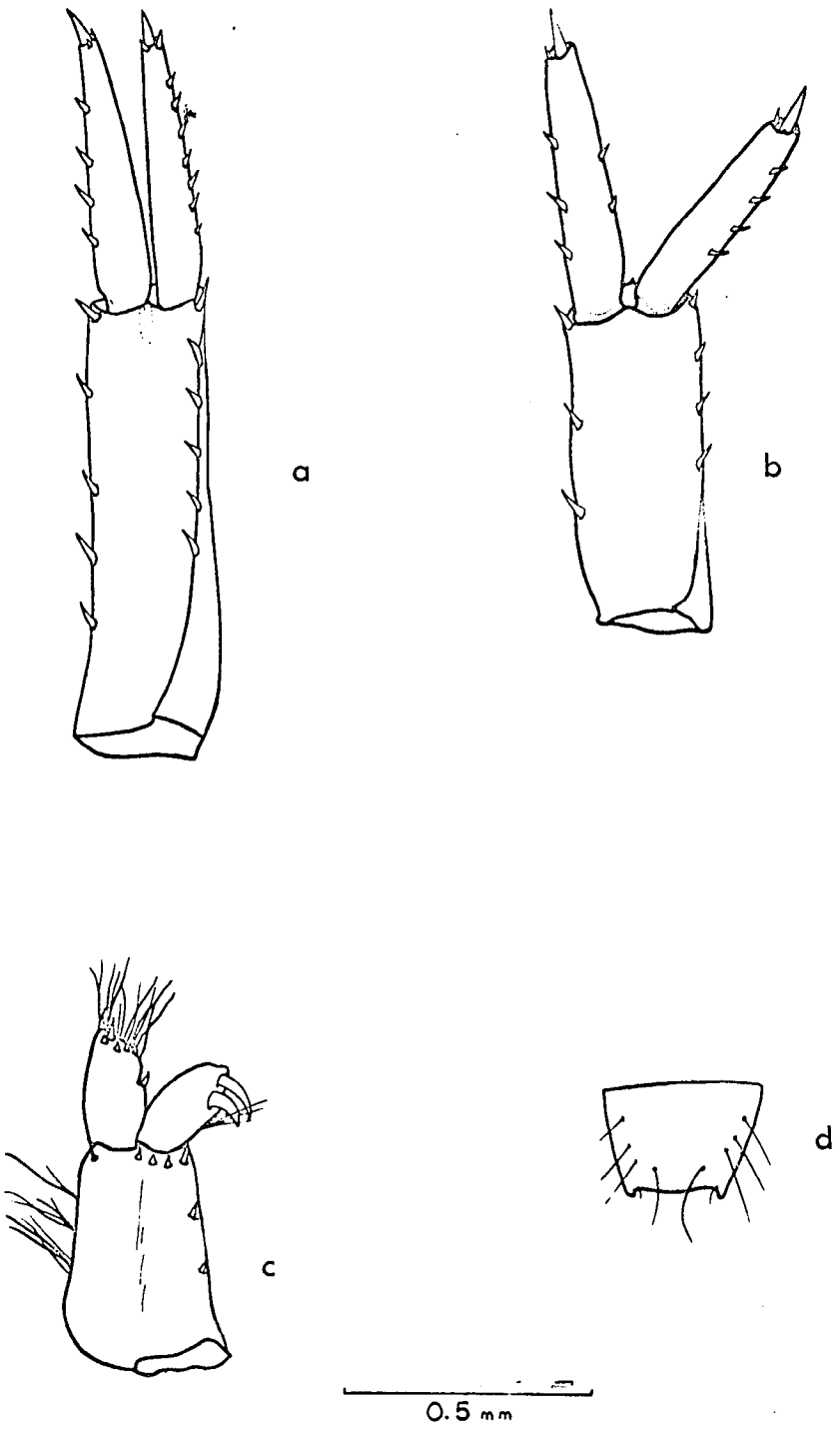

Figure III-5

Figure III-6. Comparisons of A. valida female to females of A. longimana and A. rubricata.

a. Mandibular palp of A. valida

b. Mandibular palp of A. longimana (two views).

c. Mandibular palp of A. rubricata

d. Maxillipedal palp of A. valida

e. Maxillipedal palp of A. longimana

f. Maxillipedal palp of A. rubricata

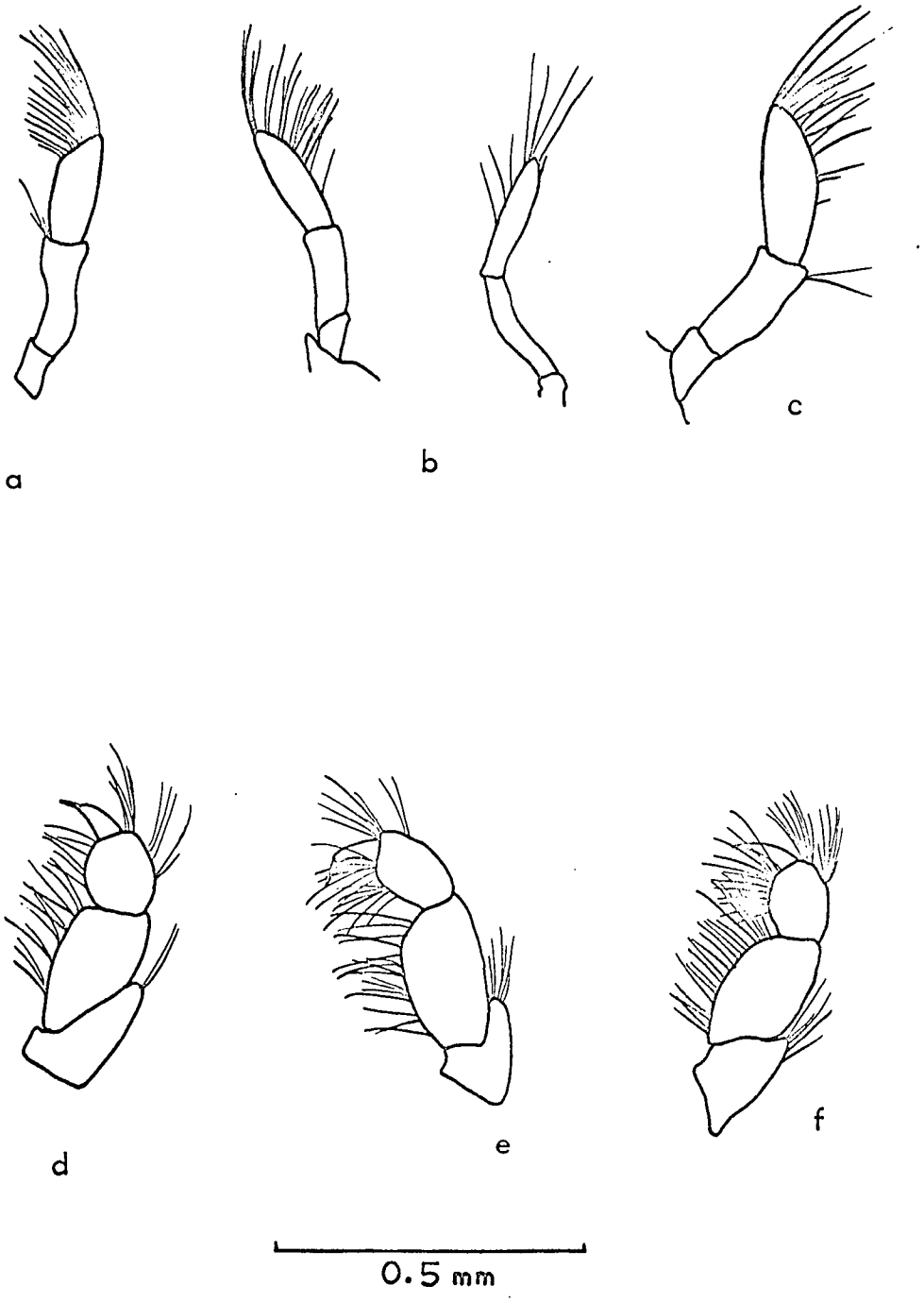

Figure III-6

Figure III-7. Comparisons of A. valida female to females of A. longimana and A. rubricata

a. Gnathopod I of A. valida

b. Gnathopod I of A. longimana

c. Gnathopod I of A. rubricata

d. Pereiopod I of A. valida

e. Pereiopod I of A. longimana

f. Pereiopod I of A. rubricata

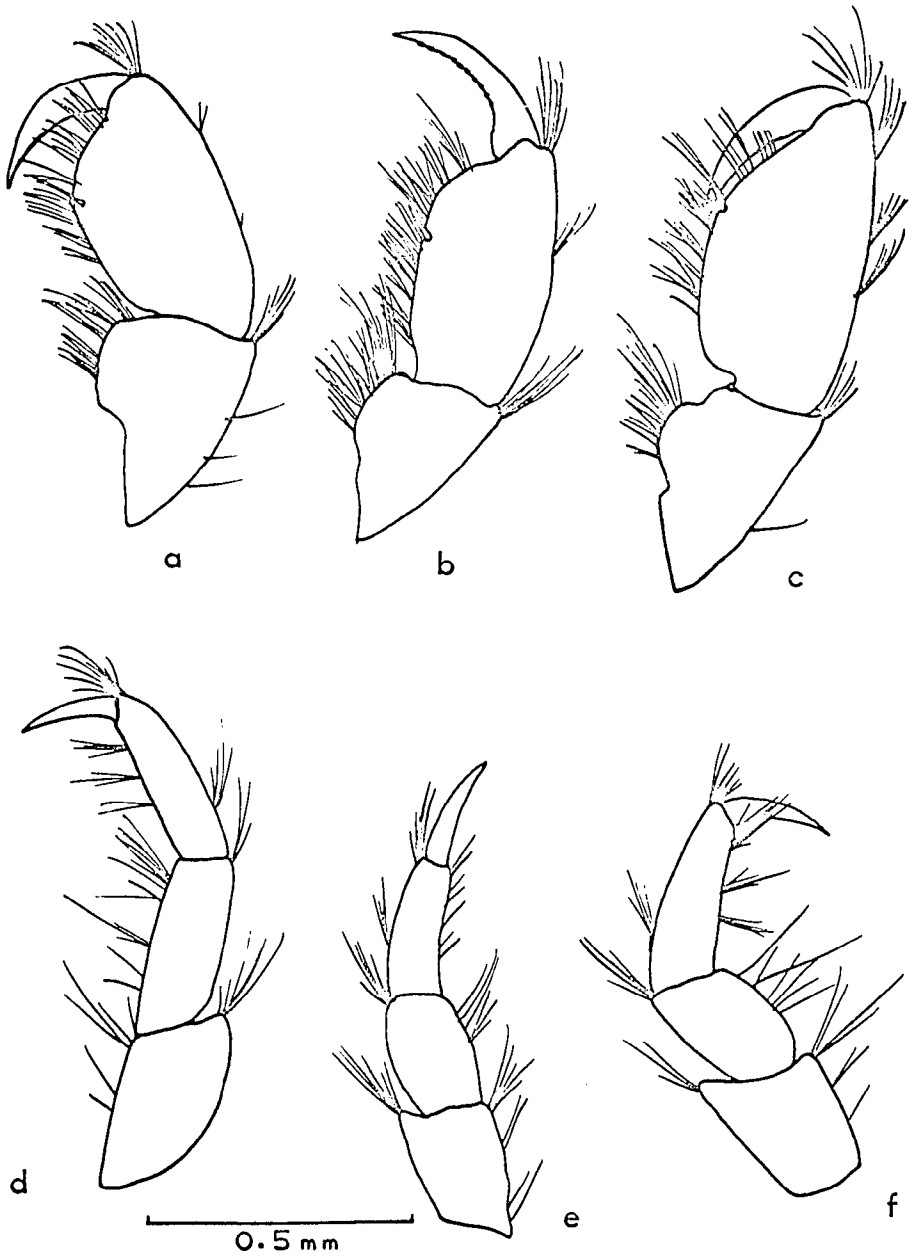

Figure III-7

Figure III-8. Comparisons of *A. valida* female to females of *A. longimana* and *A. rubricata*

a. Pereiopod II of *A. valida*

b. Pereiopod II of *A. longimana*

c. Pereiopod II of *A. rubricata*

d. Pereiopod V basis and ischium of *A. valida*

e. Pereiopod V basis and ischium of *A. longimana*

f. Pereiopod V basis and ischium of *A. rubricata*

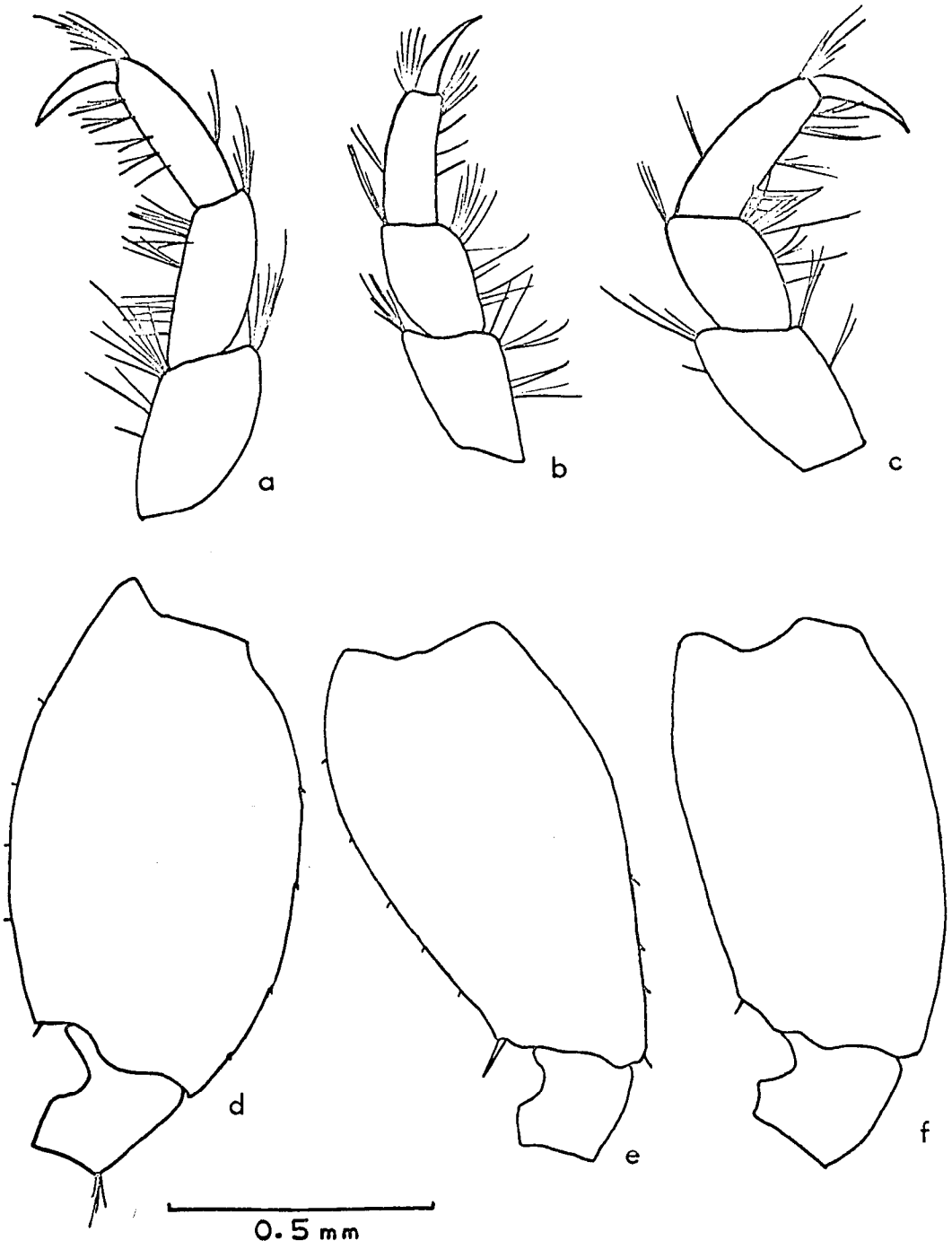

Figure III-8

SECTION IV

LIFE HISTORY

General. The sexes in A. valida are separate. Reproduction is accomplished by the union of a sexually mature male with a sexually mature female. Parthenogenesis does not occur. Fertilization must occur prior to or during ovulation. In no experiments involving females which became ovigerous without the presence of a male, did the eggs develope. The ova, in these cases, disintegrated and were lost within one week. The ovaries completely disappeared during ovulation and redeveloped during the brooding period. Upon losing the unfertilized eggs or upon the exit of the entire brood of immatures, the female moults and is ready for another brood. The moult may occur within twenty-four hours or may be delayed for as much as a week. Individuals requiring more time than a week were either moribund and died soon after or simply did not redevelop the gonads.

As in all Amphipoda, the female of A. valida broods the eggs and young in a ventral thoracic pouch formed by the overlapping of eight oöstegites. The oöstegites bear long setae along their borders which tend to become entwined to form a continuous mat. This maintains the egg mass but does not prohibit the flow of water produced by the pleopods from passing through the pouch. This fairly regular flow

of water supplies the eggs with oxygen and also moves the eggs about within the pouch. The movement of the eggs is also accomplished by the action of the thoracic appendages.

In the twenty-one experiments involving the fertilization and non-fertilization of the ova, the females were allowed to have a brood of young. The next moult and subsequent ovulation were then carried out without the presence of a male. These ova were lost in all twenty-one instances. The next moult and ovulation were then allowed to be carried out in the presence of a male. These broods, for the most part, proved to be fertile.

In the culturing of eighty-five broods involving thirty-seven females and fifty-three males, only twelve broods proved to be sterile. From these experiments and data, it is quite evident that (1) there must be copulation and fertilization to produce the young and (2) the females do not store the sperm in any manner to fertilize further broods. Excluding the fact that it might occur as an extremely rare phenomenon, it would also appear that if parthenogenesis were to occur, it would have done so. These experiments were carried out for both warm and cold water cultures.

Males which, by their total body length and the size and development of their second gnathopod (Figure IV-1), were considered to be old, failed in numerous attempts at copulation. These males were replaced by younger males which had not completed the heterogonic growth of their

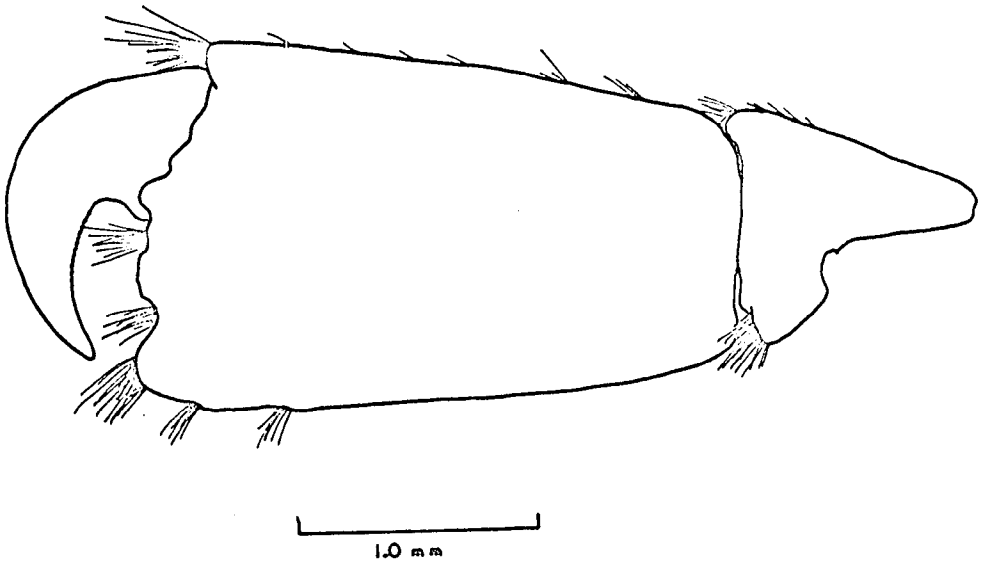

Figure IV-1. Second gnathopod of an old male showing size and development.

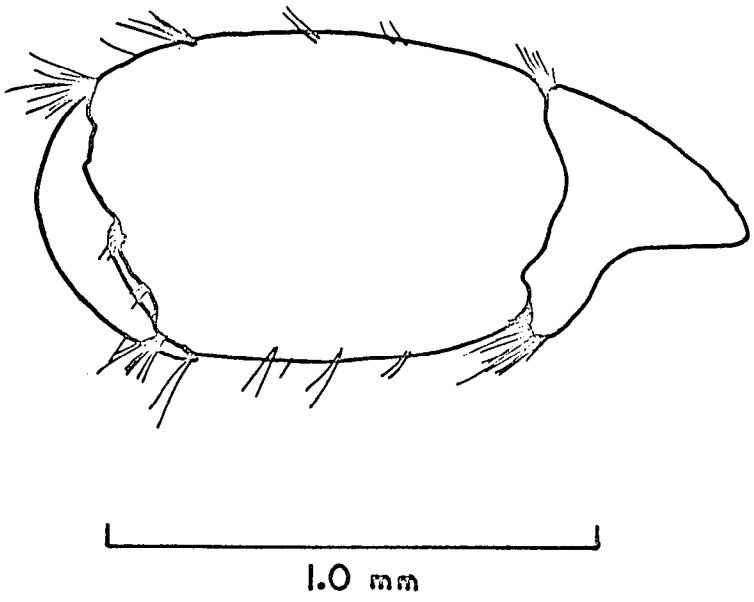

Figure IV-2. Second gnathopod of a young male showing the incomplete development of the palmar tooth and defining angle.

second gnathopods (Figure IV-2). These younger males were readily accepted by the females and copulation was completed within a few minutes after their meeting.

The processof ovulation was observed in one female. This observation showed the eggs to be laid within the brood pouch singly. The oviducts alternated for the most part, in giving forth the eggs. The eggs appeared to be fertilized upon entering the brood pouch.

Pairing and Copulation. The process of copulation was witnessed on numerous occasions during the summer months. The observations were made on individuals collected in the field and then maintained in culture.

It is commonly observed for members of the family Gammaridae that the male pairs with and carries the female prior to copulation. Holmes (1901a) pointed out this phenomenon for A. longimana. This trait was never observed in the field nor in any of the cultures of Ampithoe valida. The male lives separate from the female for most of its life span. There are some exceptions to this which are discussed later. Skutch (1926) makes no mention of any pairing and transporting of the female by the male for A. rubricata (Montagu).

The pair locate one another by what appears to be chance. If the female has just previously moulted, she will accept the male and begin the pairing and copulation ritual. This is in agreement with what Holmes (1903) stated for the recognition of sex in amphipods. He believed that this

recognition was not based on sight or chemoreception but rather on behavior. The pair will either occupy a previously constructed tube or more commonly they will begin to construct a new tube. Periodically the male will begin the ritual of caressing the female. The caressing is done by both pairs of gnathopods (Figure IV-3). In all observations, the female did not seem to be affected by these initial advances of the male. Instead, the female continued to weave the nest. Tube building and advances were temporarily disrupted for occasional periods of feeding. As tube construction continued, the effects of the male's advances appeared to have more bearing on the female's reactions. The antennae of the male are increasingly used in the caressing process.

The position held by both partners during the caressing and the initiation of copulation is the same. The female and the male face the same direction and are both vertically oriented on the same plane (Figure IV-3).

The caressing of the female by the antennae of the male follows two main themes. The first antennae tap and feel about the dorsal surface of the female. The second antennae are plied about the sides and on occasions, reach under the female and probe the brood pouch. In those cases in which they did not, the second antennae were plied along the dorsal and lateral sides of the female.

The two pairs of gnathopods are also quite active. They caress the dorsal surface of the female's abdomen and

Figure IV-3. Caressing act of A. valida showing the male dorsal to the female.

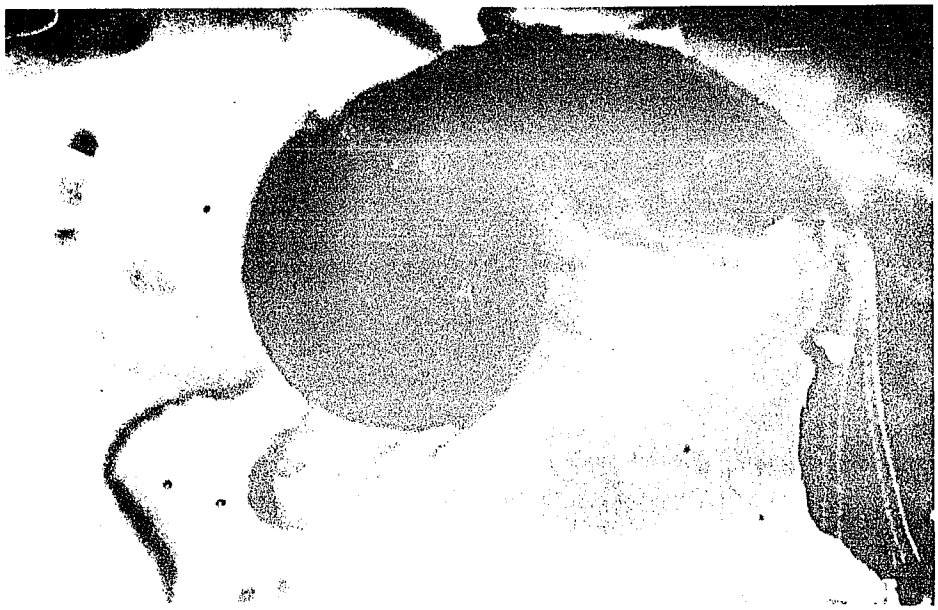

Figure IV-4. Position of copulation. Note the ovaries of the female (darkened band along the dorsal region of the pereion).

thorax at the point of flexure and anterior to that point. Their movement is quite rapid and gives the impression of vigorous scratching.

When the female becomes receptive to the advances of the male, she slowly unflexes her abdomen from the normal position until she is nearly straight. At this point, the male flexes his abdomen even more, until he has nearly completed a backward somersault. This movement places his abdomen opposite the female's. Once this position has been achieved (Figure IV-4), the male begins a series of rapid probings of the female's pleon and brood pouch with his urosome. These movements slowly subside until there are no bodily movements by either partner. After fifteen to thirty seconds, the pair separate.

Prior to the unflexing of the female, the male places his uropods tightly to the juncture of his abdomen and thorax. This movement is repeated several times.

Once the pair have separated, the female begins a rapid beating of her pleopods. Gaylor (1922) noted a similar beating in Hyalella azteca (Saussure) and believed that this was the method for conveying the sperm to the brood pouch.

The entire ritual may be repeated as many as five times within the hour, with each ritual encompassing some three to five minutes. Clemens (1950) stated for Gammarus fasciatus Say in culture this process may occur as many as thirty times. In A. valida, the female usually refuses to

accept the male after five or six attempts. Normally the ritual begins within five to ten minutes after the female has moulted. However, in culture, some females which have been isolated from males have copulated after a span of twelve hours from moulting. Likewise, on two occasions, females were brought into copula within three minutes after moulting while they were too weak to move or resist.

Within six hours after the copulatory act or acts, the female has, in most cases, completed ovipositing.

Usually after copulation the pair separate. There appears to be no set rule regarding which one leaves the nest.

In three instances females which had ovulated without the benefit of a male were observed to accept a male when he was introduced. The results of this showed that of thirty-seven eggs ovulated, only six developed. These eggs had not been in the brood pouch for more than twelve hours before the sperm were introduced. This would suggest that the eggs remain fertilizable for not much more than twelve hours after ovulation.

Egg Production and Brooding. The ovoid eggs of A. valida are somewhat similar in shape to that of a chicken egg (Figure IV-5). One hundred forty-four eggs preserved in alcohol were measured for length and width. These eggs were taken from fourteen different females which ranged in size from 7.8 millimeters to 13.1 millimeters. The females were collected in the months of

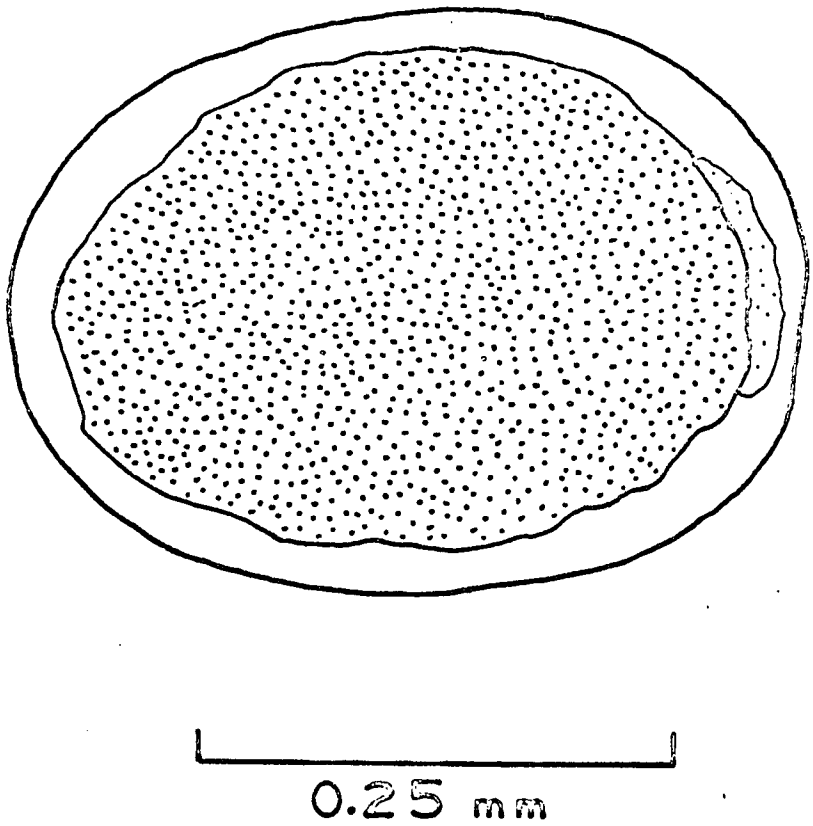

Figure IV-5. Typical fertilized egg of A. valida.

May, June, August, September and October. The mean length for these eggs was 0.46 millimeters. The standard deviation was 0.031 millimeters. The mean width was 0.37 millimeters. The standard deviation for the mean width was 0.068. A small sample of living eggs was measured for comparison with the alcoholic eggs and showed them to be within the size range of the alcoholic eggs. The size or shape of the egg does not appear to be dependent upon the size of the female, size of the brood or the time of the year.

The mean number of eggs produced by fifty-three females taken in the field was twenty-two. The range was from three to sixty. The frequency and distribution of the eggs per brood is shown in Table IV-1. This revealed a high proportion of females with five to eighteen eggs per brood. This tight grouping of females was offset by the numbers of females producing thirty to sixty eggs per brood. It was not feasible to make a comparison with cultured females. The eggs could not be accurately counted unless they were removed from the brood pouch or they were very few in number. On numerous occasions this removal was attempted and ended in the death of the female and eggs. Ovigerous females were anesthetized and thereby uninjured in the process but the eggs still died either from handling, anesthesia or the fact that they could not be replaced into the brood pouch.

During the course of study of the animals in culture, data were collected on the number of eggs produced

TABLE IV-1

Numbers of eggs produced per female in habitat

Number of eggs	Freq.	Number of eggs	Freq.	Number of eggs	Freq.
1	0	21	1	41	0
2	0	22	1	42	1
3	1	23	0	43	1
4	1	24	0	44	0
5	2	25	2	45	0
6	4	26	1	46	0
7	1	27	1	47	1
8	1	28	1	48	1
9	0	29	1	49	1
10	4	30	0	50	1
11	2	31	1	51	1
12	2	32	0	52	0
13	3	33	0	53	0
14	2	34	0	54	1
15	1	35	0	55	0
16	3	36	1	56	1
17	3	37	0	57	0
18	1	38	0	58	0
19	0	39	0	59	0
20	1	40	1	60	1

by females producing their first brood (Table IV-2). The mean production for first brood females was 4.5 eggs. The range was two to seven. These values are based on eight females reared as F_1 and F_2 generations. The smallest brooding female measured 6.3 millimeters in length.

Clemens (1950) pointed out that for Gammarus fasciatus Say, the size of the brood was dependent upon the size of the female. In this instance, the criteria of size were the body length and the pereion length. Clemens

showed a closer correlation between pereion length and brood size than between body length and brood size. Cheng (1942) utilized body weight in his study on various species of gammarids and came to the same conclusion that the larger the female, the larger the brood. The studies of the fecundity of A. valida show very clearly that size is a factor in the number of eggs produced (Figure IV-6). The coefficient of correlation for the plotted linear function is + 0.92. A "t" test was calculated and produced a "P" value less than 0.001. The females involved in this study were collected in the field and the eggs taken from them to be counted.

There is seasonal variation in the numbers of eggs produced by A. valida (Table IV-3). Clemens (1950) shows a steady decrease in the average number of eggs produced as the season progresses from April to October. Although no collections were made prior to the month of May, this table would indicate that the numbers of eggs produced was at its peak in June and that before June the numbers would be less. Similarly, the numbers decrease after June. No ovigerous females were collected during July. It is believed that this is in the realm of population dynamics and therefore it is not considered in this work. It is interesting to note that the young produced in late May and June had not, as yet, become mature by July.

The total brooding time from ovulation to the exit of all the immatures was divided into two periods. The first

TABLE IV-2

Fecundity - Fertility of
females bearing first brood

Size in mm.	Number of eggs	Number of immatures
6.3	5	5
6.5	2	1
6.7	4	4
6.8	5	3
6.8	3	1
7.0	7	6
7.1	6	6
7.2	4	3

TABLE IV-3

Average number of eggs
per month by female size

mm. Size Class	May	June	July	August	Sept.	Oct	Nov.
7	-	14.0	-	8.6	-	6.0	-
8	-	13.0	-	13.0	-	6.4	-
9	13.0	22.0	-	20.5	14	-	-
10	16.5	35.0	-	-	18	14.0	-
11	23.6	44.6	-	41.6	21	-	-

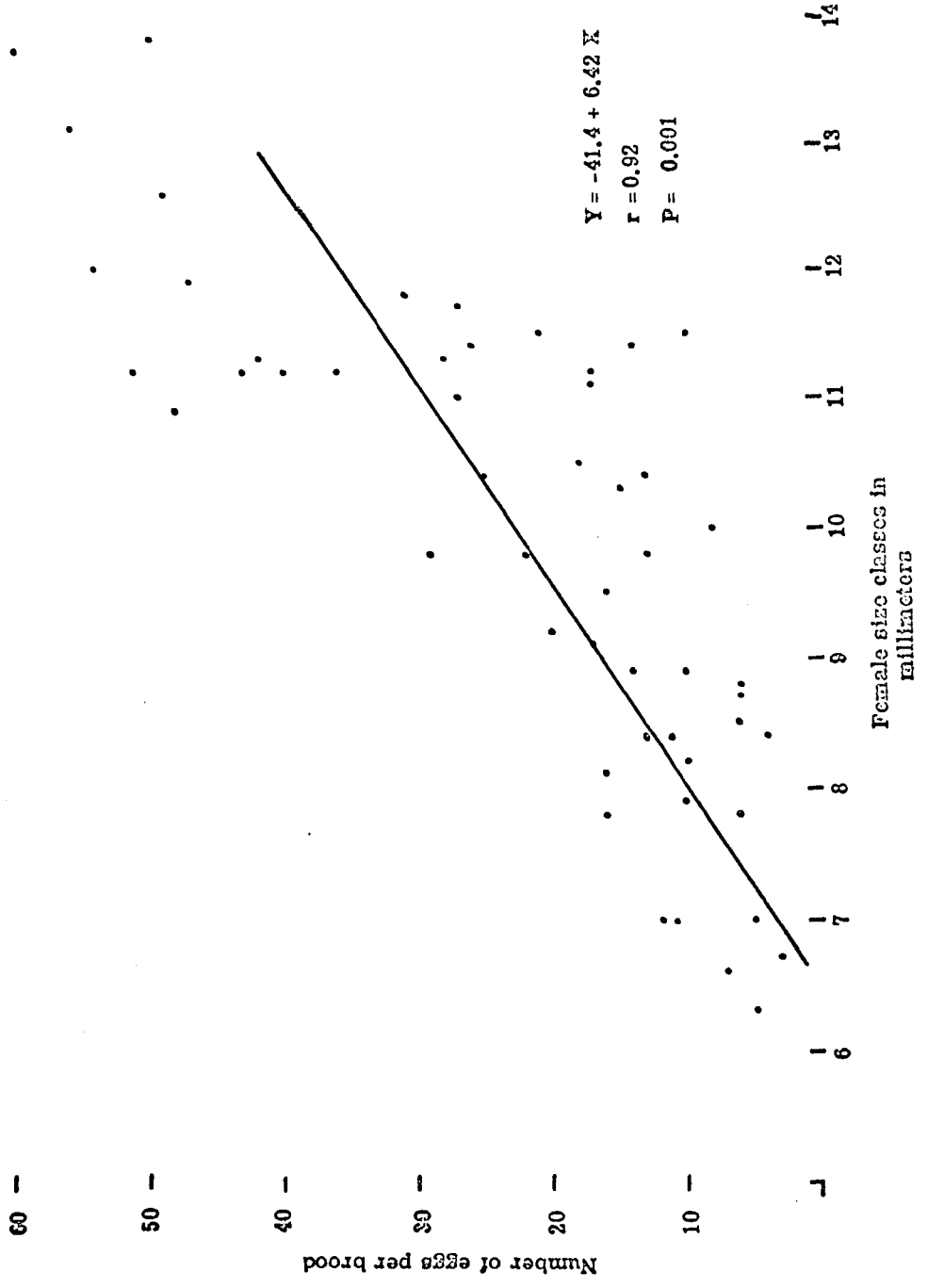

Figure IV-6. The relationship between female size and the number of eggs per brood. (Determined by field counts)

period covers the time from ovulation to the time of hatching, henceforth called hatching time. The second period covers the time from hatching to the exit of all the immatures and in this work is called brooding time.

Hatching time is greatly affected by temperature (Figure IV-7). This is easily explained by the Van't Hoff and Arrhenius Law since the temperatures did not exceed the extremes of their tolerances. In vitro and at 21° Centigrade, broods of eggs had a mean hatching time of four days which ranged from two to six days. This mean was based on thirty broods. In contrast to this, the eighteen broods maintained in vitro at 12° Centigrade averaged ten days. In this case the range was from six to thirteen days. Hatching time does not appear to be affected by the size of the brood (Figures IV-8 and IV-9). In plotting the number of days to hatch versus the number of eggs per brood maintained at 21° Centigrade, the coefficient of correlation for the linear function fitted to those plots was 0.13. A "t" test was calculated and gave a "P" value of 0.5. This makes it fairly apparent that the size of the brood has little to do with the hatching time. In cultures maintained at 12° Centigrade, the coefficient of correlation was 0.54. The "t" test produced a "P" value of 0.9 to 0.8. These values indicate even a lesser relationship.

The eggs in a brood do not all hatch at the same time. They do all hatch within a few hours of one another.

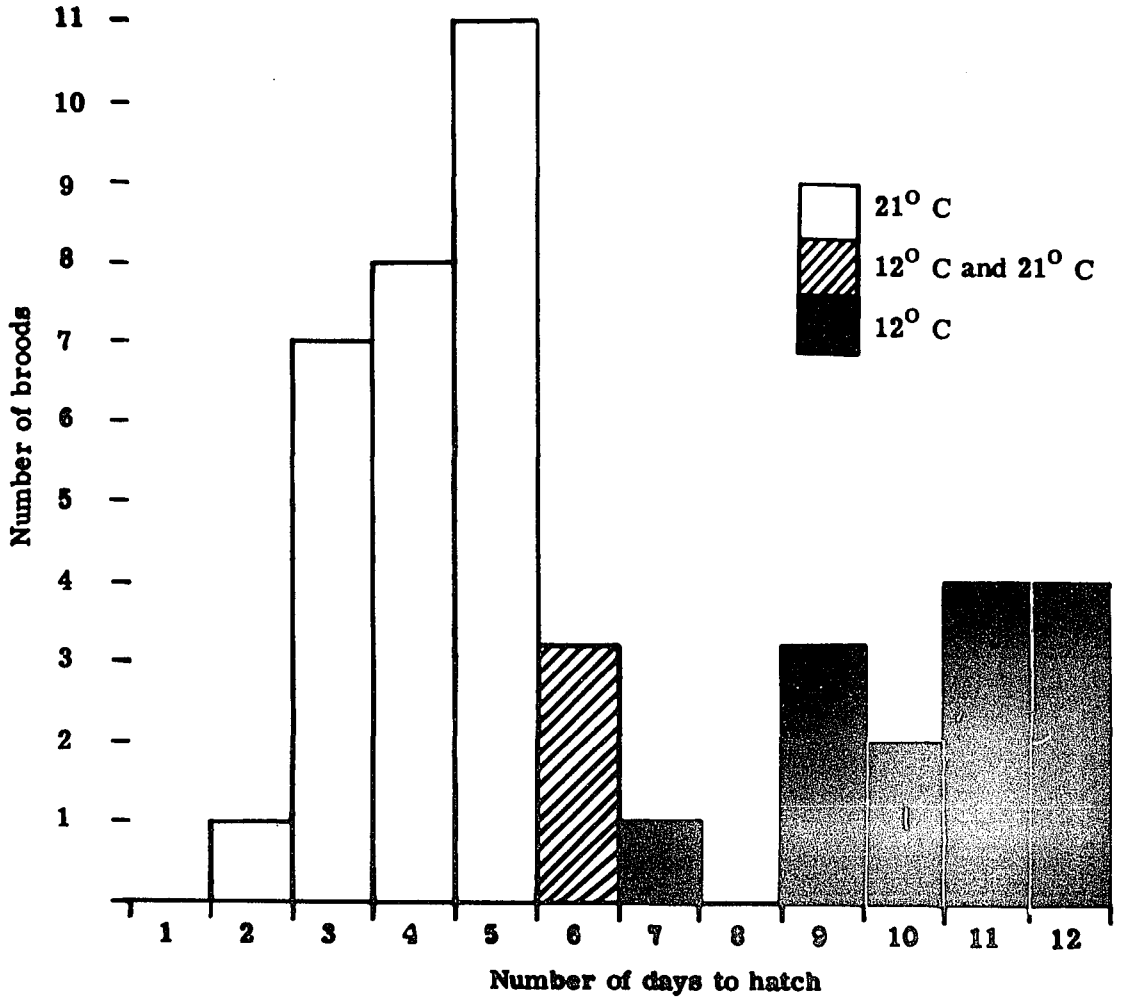

Figure IV-7. Distribution of the number of broods in relation to the time required to hatch at various temperatures.

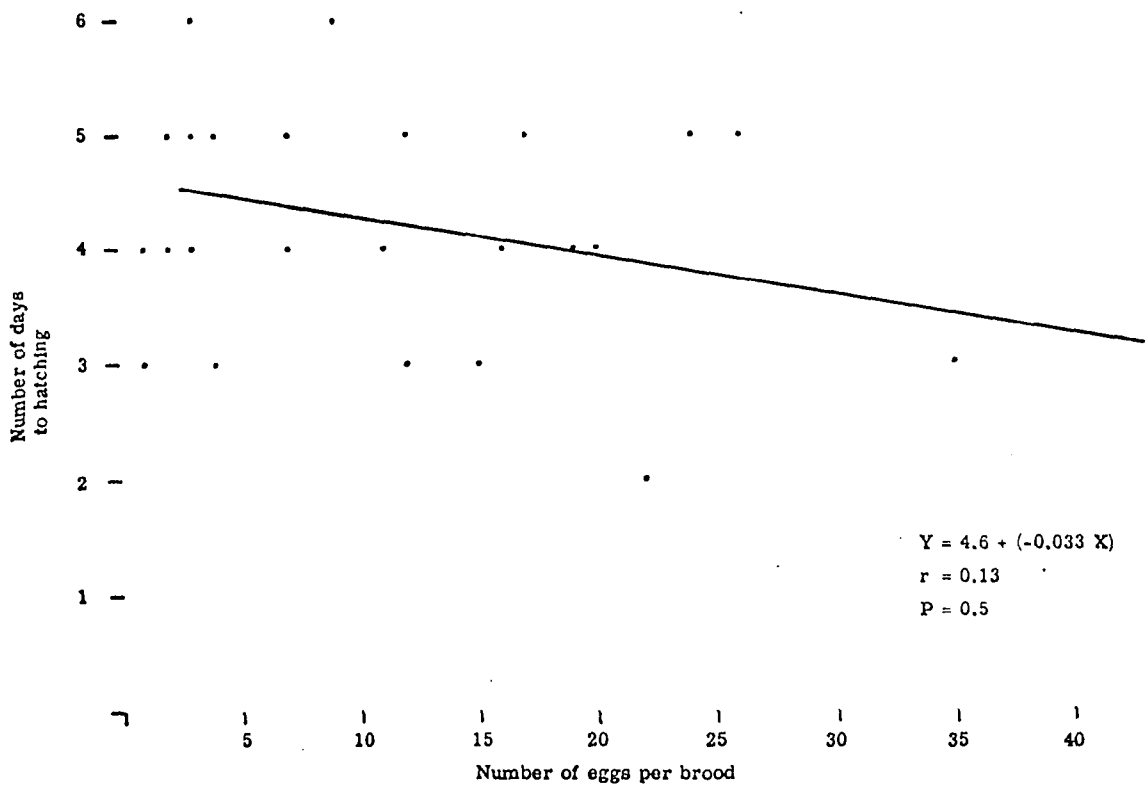

Figure IV-8. The relationship between the number of days required for the eggs to hatch and the number of eggs per brood at 21°C +10°C and -1°C.

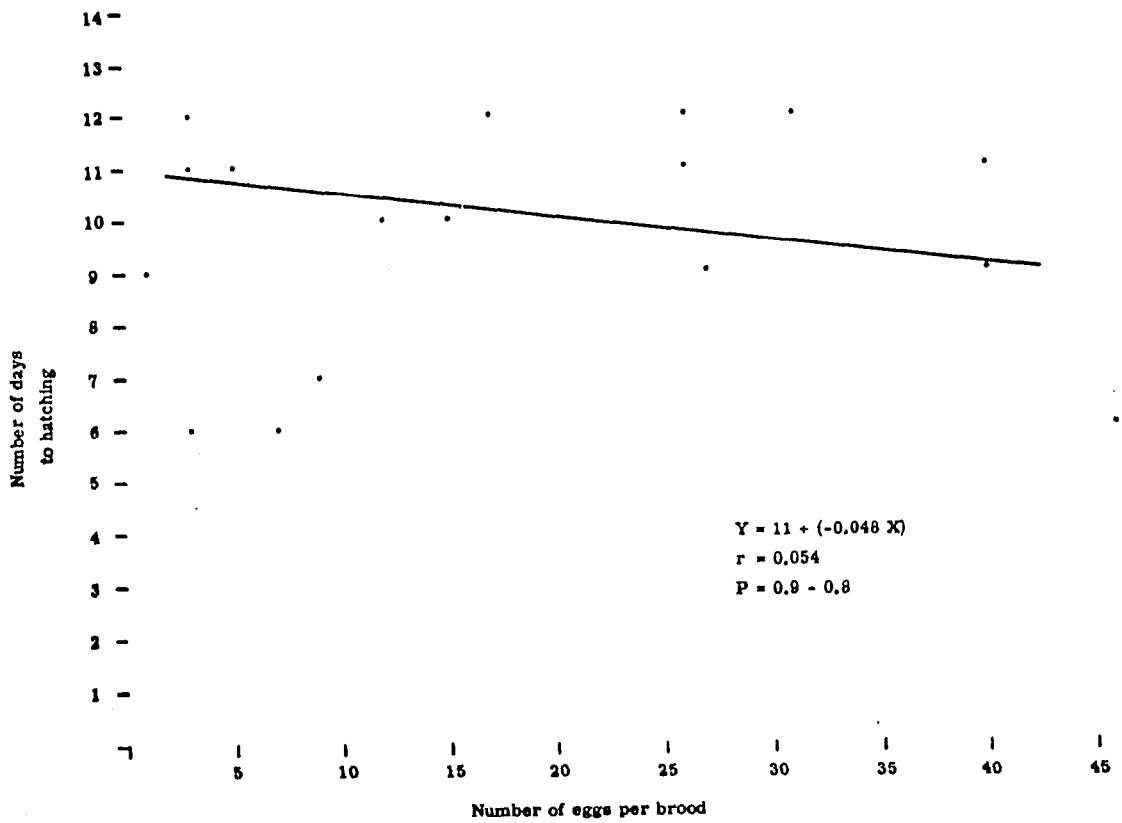

Figure IV-9. The relationship between the number of days required for the eggs to hatch and the number of eggs per brood at 12°C ±1°C.

The length of the newly hatched immature measures 1.4 millimeters ± 0.1 millimeter. Upon leaving the brood pouch, they measure 1.9 millimeters in length. Measurements were taken on sixteen immatures from within a few minutes prior to hatching to within a few minutes after hatching. The size and growth of the immatures upon leaving the brood pouch will be discussed later in Section V.

After hatching, the young remain within the brood pouch for varying lengths of time. This period of time appears to be dependent upon one factor. This is temperature (Figure IV-10). Although there is a large degree of overlap within the histogram, it is believed that this is due to the interaction of a number of factors. These are possibly low numbers of samples, culture induced problems and even the fact that the lower limit of temperature for brooding has been approached. In view of the latter, it is interesting to note the loose similarity between this histogram and that of the one involving hatching (Figure IV-9). The mean brooding time for cultures maintained at 21° Centigrade was four days with a range of two to seven days. In contrast to this, the mean time for cultures maintained at 12° Centigrade was seven days. The range was three to fifteen days.

Brood size, as in hatching time, appears to have no effect on the length of brooding time (Figure IV-11 and IV-12). In both the cultures maintained at 21° and 12° Centigrade, the coefficients of correlation were low.

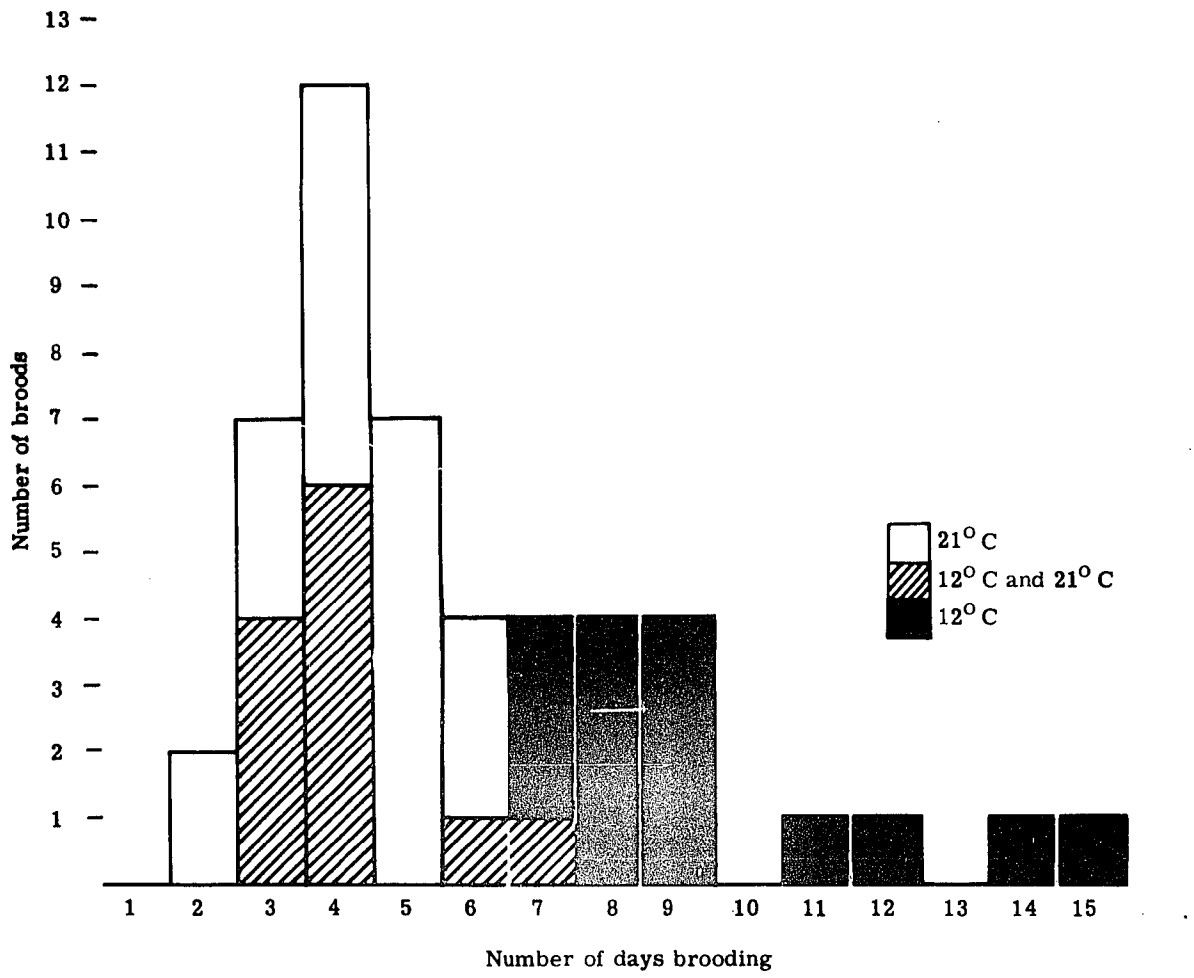

Figure IV-10. Comparison of the number of broods to the number of days the immatures remained within the brood pouch at 12°C ±1°C and 21°C +10°C and -1°C.

They were 0.37 and 0.36 respectively. The respective "P" values for these were 0.025 and 0.1 to 0.05.

The number of immatures found in the first broods of the eight previously mentioned females ranged from one to six. A comparison of the size of the female, number of eggs in the first brood and the resulting number of immatures may be seen in Table IV-2.

Females in vitro at 21° Centigrade produced a mean of 2.3 broods. This was based on seventeen females which had ovulated, brooded and ovulated again. At 12° Centigrade, seventeen females produced an average of 1.7 broods. The maximum number of broods produced by a female maintained at 21° Centigrade was nine and for a female maintained at 12° Centigrade it was four.

As would be expected, from the number of eggs being dependent upon the size of the female, the number of immatures is also dependent upon the size of the female (Figure IV-13). The data for this graph were taken from counts of immatures brooded by females in vitro. The coefficient of correlation for the linear function is 0.695. The "P" value being less than 0.001.

Although no concrete conclusions as to the exact ratio of fecundity to fertility can be drawn, other than that the percentage decreases with an increase of female size, a plotting of the linear functions of Figure IV-6 and IV-13 shows that there is a direct relation (Figure IV-14). It is not possible to collect females bearing

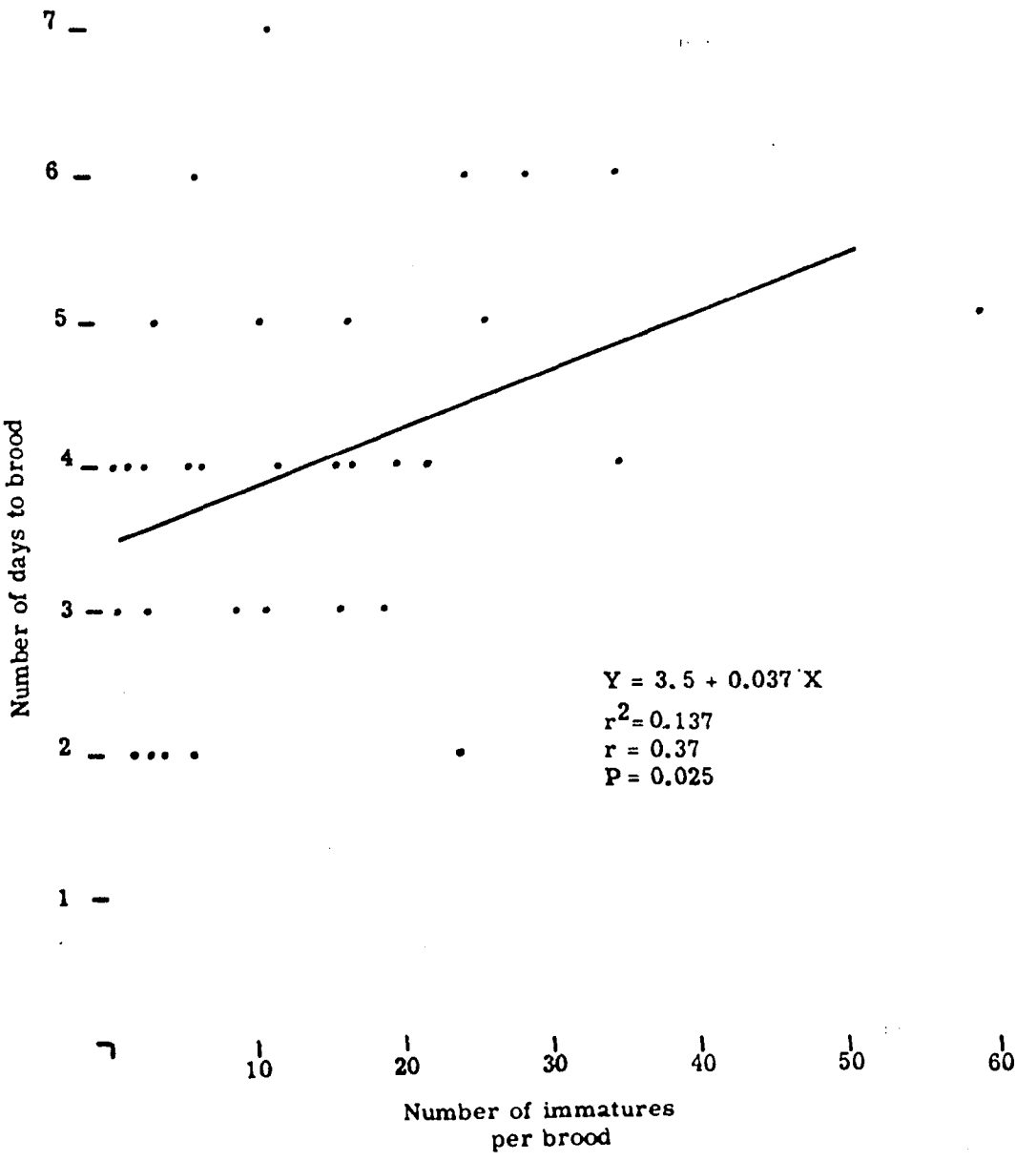

Figure IV-11. The relationship between the number of days brooding and the number of immatures maintained at 21°C +10°C and - 1°C.

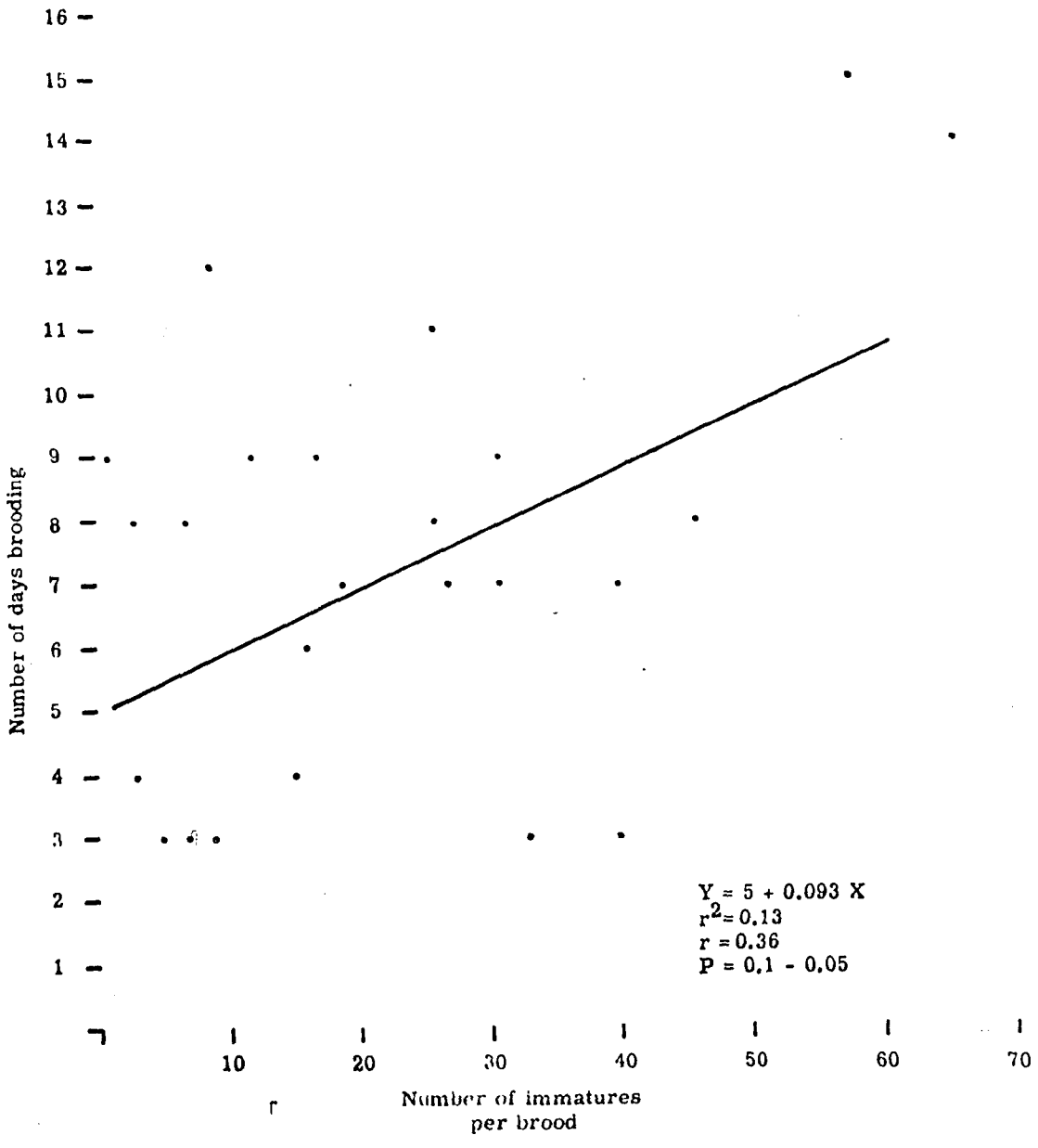

Figure IV-12. The relationship between the number of days brooding and the number of immatures per brood maintained at 12°C ± 1°C.

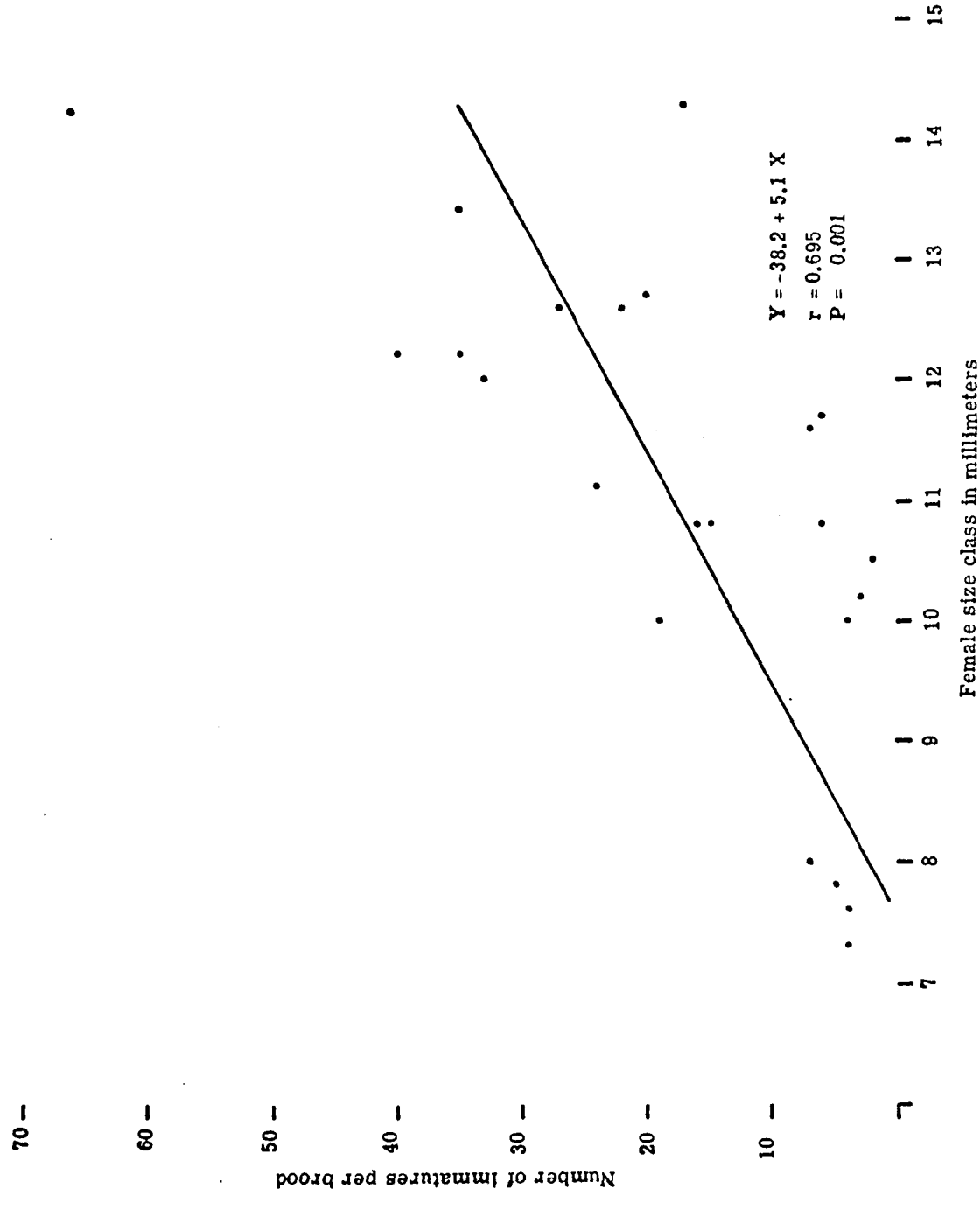

Figure IV-13. The relationship between the number of immatures and the size of the female. (Brooded in culture)

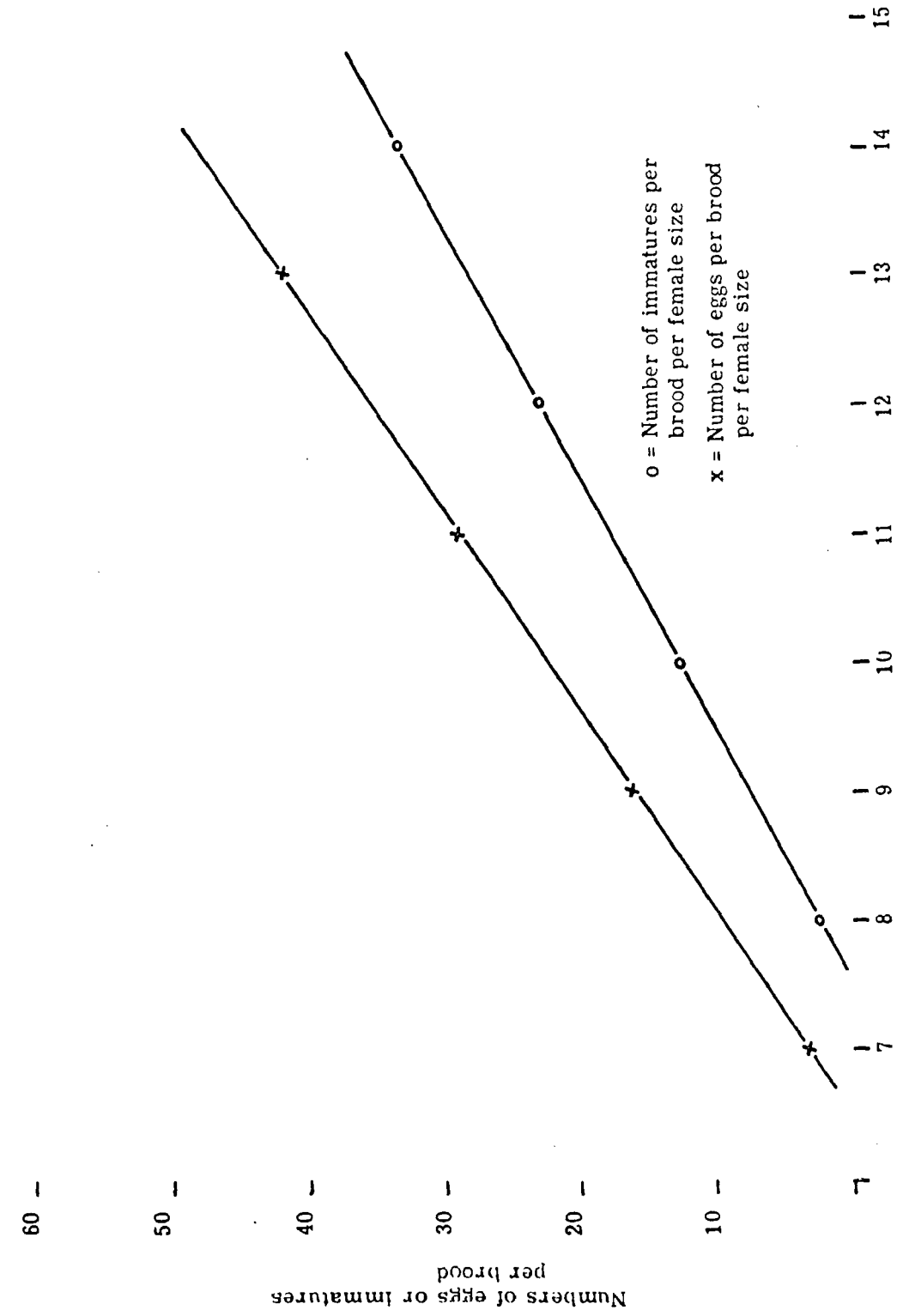

Figure IV-14. Comparison of the numbers of eggs and immatures produced to female size.

immatures in the field and be certain that some of the already hatched immatures have not left the brood pouch. Immatures do not all leave the pouch at the same time, but rather straggle out a few at a time over a period of one to three days.

SECTION V

HABITS

Studies of the habits of A. valida were performed primarily on the animals maintained and raised in culture. Comparisons between the culture observations and field observations showed that there was little, if any, observable difference in the animals' behavior in the two situations. Culturing enabled observations to be made at any given time.

The habits or behavior patterns most closely scrutinized were nesting and tube construction, swimming, crawling, various tactic behavior and feeding.

Movements. A. valida moves about its domain utilizing two primary methods. The most commonly utilized method is that of crawling or walking. In this respect, they give one the impression of rats. Walking is accomplished by the use of the second antennae, first and second pairs of gnathopods, and the first two pairs of pereiopods. Coupled with the use of these structures is the occasional use of the abdomen. The functions of various appendages are all somewhat similar except for that of the second antennae.

The second antennae, in conjunction with testing the area, are utilized in such a manner as to hook on to vantage points and pull the animal forward. Holmes noted this use of the second antennae for A. longimana.

The gnathopods are used for grasping and pulling the animal forward or merely to maintain a position. The first two pairs of pereiopods move similar to, as Holmes stated:

> the walking legs of an insect, although they move in a nearly vertical plane.

The pereiopods serve one other function which aids in crawling. If the animal comes in contact with smooth surfaces which do not afford a foothold, it immediately begins spinning a network of fiber which it uses as footholds.

The appendages and their functions in crawling are in agreement with Holmes' description for A. longimana. It was observed for A. valida, but not mentioned by Holmes for A. longimana, that the animal is quite cautious while crawling about and makes frequent stops. At this time, both antennae are moved about through the water as though searching for some source of danger. Having apparently satisfied itself that there is none, the animal continues on its way. While the animal is out of its tube and moving about, it will inspect every crevice and opening that it encounters.

The other mode of locomotion commonly observed is swimming. A. valida, as with other tubiculous amphipods, is not noted for its sustained swimming ability. It is capable of short and rapid spurts of swimming alternating with brief rests or short periods of crawling. Swimming is usually only employed as an escape mechanism. However,

on occasion and for no observable reason the animal will interrupt its walking for a short burst of swimming.

Swimming as observed in A. valida is very well described by Holmes (1901a) in his description of this phenomenon for A. longimana. Although living A. longimana have not been observed and it is not known for certain that Holmes was working with correctly identified material, his description below is accurate for A. valida. He stated:

> The beat of the pleopods tends to propel the body not in a straight line forward but in a circular course. The pleopods being on the ventral side tend to cause the body to veer around towards the dorsal side. When the body is held somewhat concave on the ventral side, as it often is, this tendency may be balanced or overcome by the tendency to move in circles in the opposite direction. Such a condition is analogous to a person rowing on one side of a boat with the rudder turned towards the side of the oar. By having the body extended to the right degree a straight course may be maintained. The directions of movement is often changed by the animal turning now on one side and now on the other. Circular movements in one direction are thus compensated for by circular movements in another as the animal turns over and a certain general direction of motion is maintained. When swimming on the back a nearly straight course is kept by rolling the body slightly to the one or other side. Rolling is probably effected by the movements of the hinder pairs of thoracic legs. When the animal is swimming these legs project outward and backward. A downward stroke of these appendages on one side would push the same side of the body upward and roll it over toward the opposite side. In a larger species of amphipod, whose movements are not exceedingly rapid as those of Amphithoe, I was able to see that the rolling of the body was effected in just this way. It is highly improbable that in Amphithoe a different method would be employed to produce the same result. However this may be, it is certain that Amphithoe steers itself while swimming by altering the extension of the abdomen and by rolling from side to side. Lateral bendings of the body could not be seen to play a part in directing the swimming motions, although I have observed this method of steering employed by other amphipods.

A. valida employs its first pair of gnathopods as well as the maxillae and the maxillipeds as preening organs for the antennae. The antennae are reflexed back and grasped by the first pair of gnathopods. Whereupon they are drawn outward through the setaceous palm and the dactyl. This process is usually repeated two to four times for each antenna. This, as Holmes noted, appears to be sanitary in function. This act was repeated more often when the animals were subjected to silty conditions or if strands of their nest fibers were entangled in the antennae. This cleansing action removed debris from the antennae. It was observed that the flagella were lightly held by the previously mentioned mouthparts while being drawn through the gnathopods. Any material scraped off in this process is apparently tested for edibility.

One of the most striking movements performed by A. valida is that of reversing its position within the tube. Members of this family are well adapted for this procedure by the development of a pair of hooks on the exopodites of the third pair of uropods. Coupled with these hooks is the direction in which the last three pair of pereiopods face (Figures IV-1 and V-1). This process has also been described in good detail by Holmes (1901a) for A. longimana and applies equally well for A. valida. Holmes' description of this process is as follows:

> As the animal lies in its nest the abdomen is bent forward and the posterior pairs of thoracic legs are directed backward, their claws being usually

> hooked into the walls of the nest. When about to turn around, the abdomen is thrust forward, its terminal hooks caught in the nest; the tip of the abdomen, therefore, forms a fixed point, and the insertion of the thoracic legs forms another. The contraction of the legs would therefore pull the middle and anterior parts of the body backward. When the head is pulled back some distance, extension of the body occurs, forcing the anterior part of the body through to the other end of the nest. The head end being reversed, the abdomen is loosened and quickly flexed again under the body.

Second to the beating of the heart, the beating of the pleopods is the most constant movement performed by A. valida. The rate varies with the physiological state of the animal. When in the resting position, which will be discussed later, the rate is reduced. When in the excited state, the rate is much more constant and rapid. The pleopods create the current of water which flows around gills and, if a female, through the brood pouch. It is through their action that swimming is accomplished. The rate of pleopod beating closely coincides with the heart rate. As the heart rate slows, the pleopod rate slows and vice-versa. Halting in the beating of the pleopods does not usually last longer than one minute. The usual period of quiescence is on the average of ten seconds for adults. As would be expected, the immatures show a higher rate of beating than do the adults. The rate for an excited immature averages twenty beats per four seconds or 300 per minute. These figures were taken for immatures measuring three millimeters in length in a culture containing twelve individuals at a temperature of 22.2°C. In

comparison to this, an eleven millimeter adult averaged 210 beats per minute for the same set of conditions.

Burrowing habits have not been observed for A. valida. In six experiments in which the amphipod was placed in culture dishes conatining sand, silt or mud, the individuals always built their nests in the Ulva. If there was insufficient Ulva for nest building, they would then use the sides of the culture dish at the substrate-glass interface.

A peculiár movement exhibited by members of this species is one which resembles that of a sparring boxer. The body is extended out of the tube and reflexed back making the dorsal surface concave. The gnathopods are extended out and a series of thrusts and jabs are made. This is usually observed when an intruder to the nest is near, a newly moulted female is near or there is a gentle disturbance. Occasionally this action is observed for no apparent reason. This action may possibly be the same as one described for Ampithoe longimana by Holmes. However, his description conveys a less pugnacious tone.

Nesting and Tube Construction. Ampithoe valida, like many species of Amphipoda, is equipped with mucous glands in the first two pairs of pereiopods. These glands supply the secretion by which they construct their tubes, make footholds and retain food within the nest. Various algae and other materials have been listed by Skutch (1926) as being suitable sites for the nest of A. rubricata

(Monatgu). Holmes (1901a) briefly described the nesting habits of A. longimana. In 1874, Smith mentioned a number of amphipods including Amphithoe maculata which are equipped with these mucous glands. This species is placed in a dubious category by Barnard (1958).

The tubes or nests of A. valida are always open at both ends. This provides a double exit for the occupant. A cross section of the tube reveals that it is slightly elliptical. The size of the tube varies with the size of the occupant. Very seldom does a small individual occupy a tube much larger than itself. It has been noted in this study that immatures inhabiting the tube of the parent female have built tubes of their own within the older and larger tube. Skutch in his 1926 article on A. rubricata noted that the female forcibly evicts the immatures as they leave the brood pouch. This does not appear to be the case with A. valida. There have been occasions where the female has left the offspring in her old tube to build a new one.

Skutch (1926) stated that A. rubricata is loath to leave its tube and does so only under the most dire circumstances. His few observations of individuals out of the tube proved them to be moribund. This lack of leaving the tube is not so evident for A. valida. Both Holmes (1901) and Smith (1872) mention members of the genus Ampithoe crawling about, out of their tubes, as was observed in this study. The individuals observed in this study were not all moribund.

Females which are brooding young appear to be the most loath to leave their tubes. Once they are evicted they immediately begin construction of a new tube, providing an empty tube of a suitable size is not readily available.

Individuals build their own tubes and live in them separately for the most part. One noted exception to this solitary mode of life is in the case of pairing couples. In these cases, the male either helps in the construction of a new tube or moves in with the female. They remain together until fertilization is completed, whereupon one of the two leaves the tube.

The primary site and base material for the tubes of A. valida is Ulva. A fold or roll in the blade near the base of the plant is usually chosen. However, immatures may be found near the edges of the blade in curls or rolls of the blade. The first and second pairs of pereiopods are usually used simultaneously in spinning the web of fibers. They may be seen to alternate occasionally. The animal moves in and out the length of the prospective tube weaving a silken mat of mucous threads. These threads are not spun the same length as the tube but are anchored to the Ulva and one another at various points. These threads run parallel to the long axis of the animal and at varying angles to this axis. The threads may begin at one entrance and go to the middle or any other such combination of attachment.

The animal rotates about its long axis several times during the construction of the nest which results in a tube that is of equal density and strength. The animal also repeatedly reverses its direction within the tube during its construction. Within fifteen minutes to one half an hour a recognizable tube has been constructed. This is in agreement with Holmes' observation for A. longimana. However, as Skutch (1926) noted for A. rubricata, the animal continues to work on the tube for several days. It must also be said that on occasions, as soon as the animal has completed one tube to some extent, it has left that tube to start another or moves into one previously constructed.

Although Ulva is the primary site for the tubes of A. valida, it has been reported by Nagle (unpublished) that the animal was found in dead Spartina. In this study, individuals have been found on various occasions on Ascophyllum from Nannie Island in Great Bay. However, very few tubes were found and a great number of individuals were found. Near the Ascophyllum there is a large bed of Ulva from which these individuals may have originated. Also mixed in with the Ascophyllum was some Ulva. This latter Ulva did not show enough dwellings to support the size of the population found. It is believed that these individuals may have had their tubes in the substrate which were either destroyed upon collection or completely overlooked as something else. A possible explanation for this problem

was mentioned in section II in relation to the cement blocks.

Both Holmes (1901) and Skutch (1926) pointed out that A. longimana and A. rubricata incorporate foreign materials into their tubes. This facet of nest construction has never been reported or observed for A. valida. A. valida does include, at times, pieces of Ulva and edible substances which are separate from the blade being utilized for the nest. These items do not appear to be an integral part of the nest but rather serve as reservoirs of food. They are lightly attached and usually promptly consumed. Holmes (1901) mentioned that Smith observed, in Microdeutopus, fecal pellets being incorporated into the construction of the nest. In agreement with A. valida he stated for A. longimana:

> but in Amphithoe, whose nest-building habits seem to be very similar, no such process could be observed. The excrement is passed out of the nest, accumulations of it usually being observable near the two ends.

In support of this statement for A. valida see figure V-1. One exception to this is discussed later in this section.

Various attempts at enticing A. valida into incorporating materials other than the base material all proved futile. The only material which could possibly be said to have been incorporated was silt. It is felt that this was incidental to the construction of the tube due to the sticky nature of the fibers upon first leaving the dactyl.

Once the tube has been completed, the animal remains within it for the most part. Two major positions have been observed for the animal while it is in the tube. The first position is held with the second antennae reflexed back and under the body. The first antennae are held erect and directed out through the opening of the tube (Figure V-2). This appears to be the resting position, as the individual does very little moving about. The rate of heartbeat is reduced as is the rate of pleopod beating. The second and most commonly observed position is held such that both pairs of antennae are erect and directed out the opening of the tube (Figure V-3). This position could be named the "alert position". The heartbeat rate and pleopod rate are accelerated and the entire animal appears to be in an excited state. The alert position is most often encountered when different food is gently offered or there has been a disturbance of the tube.

The species will inhabit glass as well as plastic tubing, providing the inside diameter is of sufficient size to allow the animal freedom of movement. In testing the animal for thigmotaxis, this was clearly demonstrated (Figure V-4). Individuals were still inhabiting these artificial nests several days after their introduction and with a good supply of Ulva present. Unless larger bore tubing is supplied, growth will demand their eviction. The individuals living within the tubing lined it with fibers and carried on all functions normally.

The removal of fecal material is accomplished by thrusting the abdomen anteriorly so as to place the anus within the reach of the mouthparts and gnathopods. The fecal material is grasped by these appendages and the abdomen is then pulled posteriorly by the extensor muscles of the abdomen and thorax. This movement literally pulls the fecal material from the rectum. The material is tested for edibility and then either eaten or pushed out of the tube by the gnathopods.

Tactic Behavior. A. valida exhibits many innate behavioristic patterns which are tactic in character and appear to be common for most gammaridean amphipods. The tactic behavioral patterns discussed below are similar to those observed in Gammarus fasciatus by Clemens (1926) and in A. longimana by Holmes (1901a).

A strong thigmotactic behavior is exhibited. If left alone in a culture dish with nothing but the culture water, the animal will swim about for a short period of time and then come to rest. The resting site is usually at the bottom of the dish where the side joins, or at the surface where the water and the side meet. The side-bottom region affords a curvature which increases the surface in contact with the animal over that of just the bottom. It was noticed that this region was usually utilized if the dish was clean and had no tube fibers along the sides. However, if the dish was one which had not been scrubbed clean and had tube fibers along the

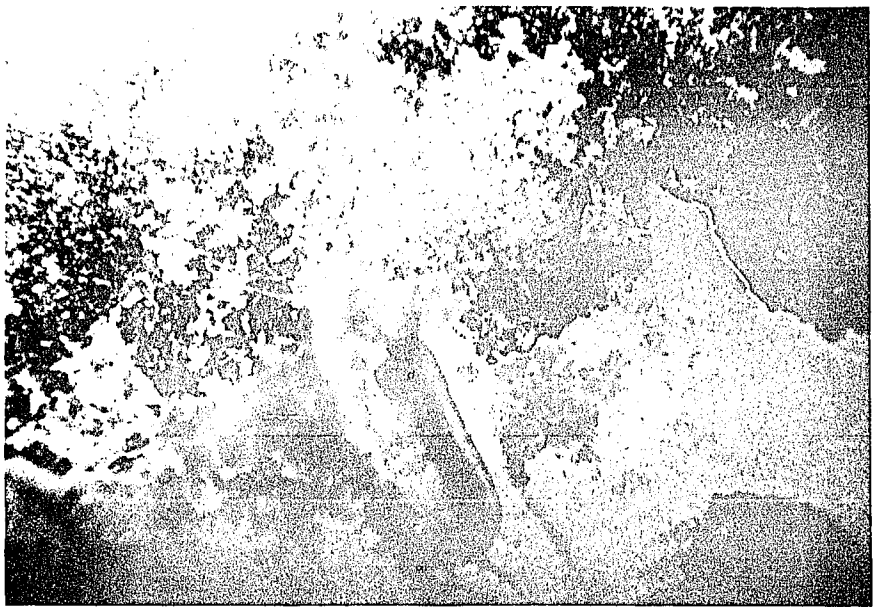

Figure V-1. Photograph showing A. valida in its tube with fecal material outside the tube around the entrance.

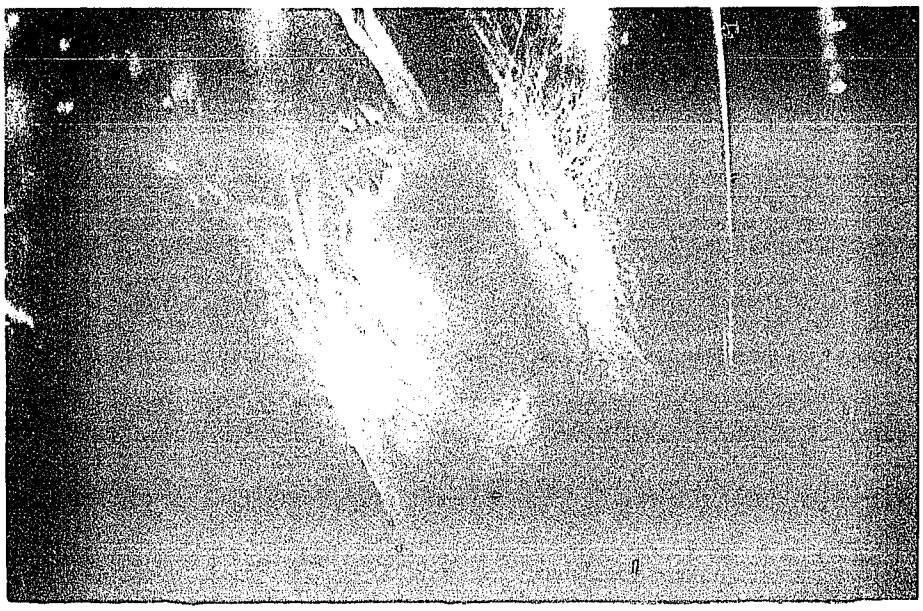

Figure V-2. Photograph of a male A. valida in the "resting" position.

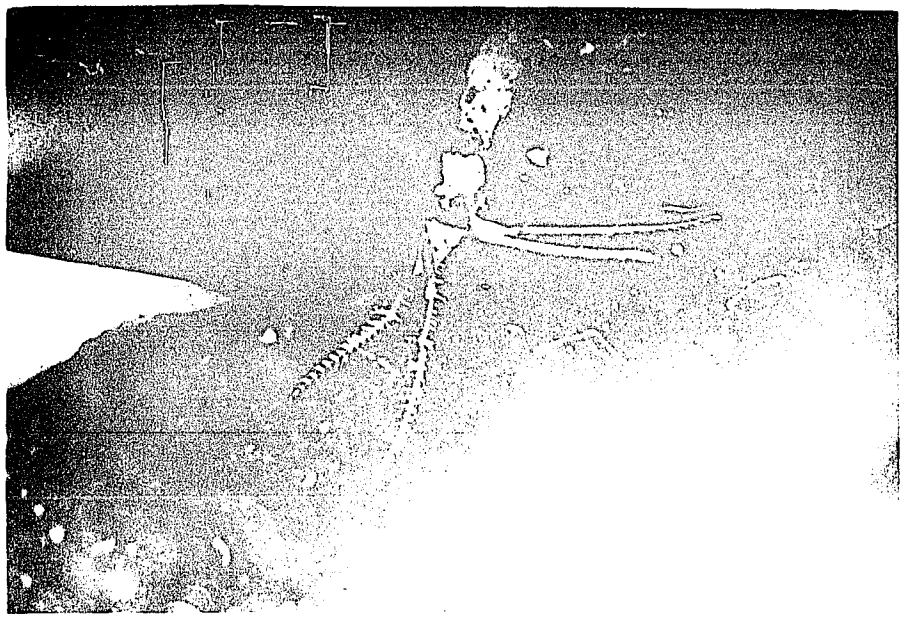

Figure V-3. Photograph of A. valida in the "alert" position.

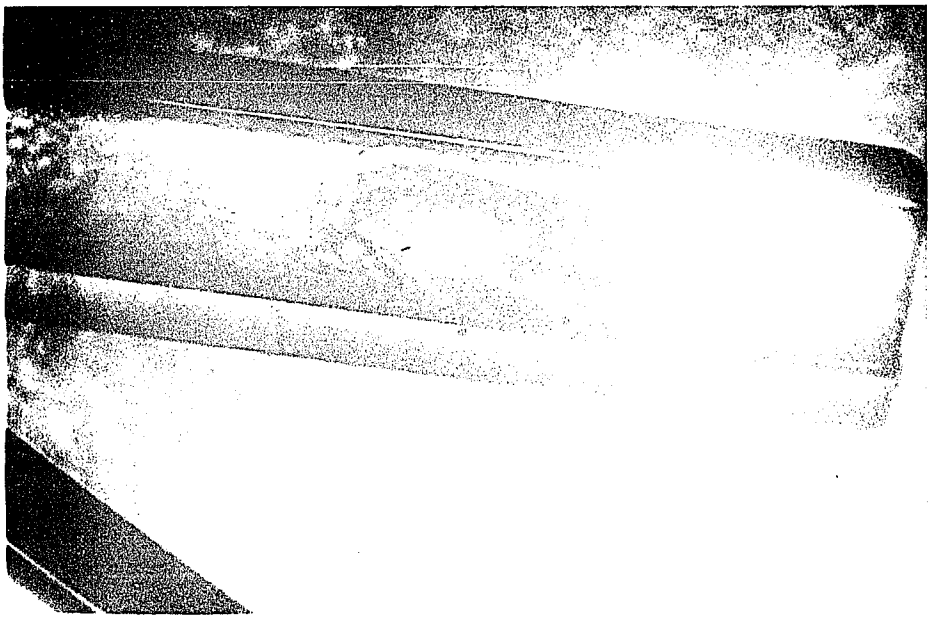

Figure V-4. Photograph of a male A. valida inhabiting a piece of glass tubing.

sides, then the animal usually chose the surface-side angle. This position afforded the side of the dish and the surface tension of the water as two regions of contact. The periods of resting are short in duration and the animal appears to be very uneasy.

Short pieces of glass and plastic tubing were placed in the culture dishes. These were the only items in the dishes which afforded protection. Within fifteen minutes after the tubing had been introduced, the amphipods had moved into them and had begun weaving their fibers. Territorial rights were established and any intruder was viciously fought off. It is interesting to note that the first individual to test and enter the tubing was an ovigerous female. As pointed out prior to this, the ovigerous female is the most loath to leave her nest. It is only speculative, but it appears that the condition of being ovigerous increases the thigmotactic behavior of the animal.

Once the animals were established within the tubing, they were offered small pieces of Ulva. They readily accepted these and began feeding. The Ulva was lightly attached to the tubing at the entrance and could not be considered a part of the tube. The animals and their tubing were then placed in the original culture dishes containing adequate Ulva and nests. After one hour had elapsed, an inspection was made which revealed that all individuals were still in their respective tubings. After another four hours all individuals were still in their

respective tubings. After still another four hours seventy-five percent of the individuals were still within the tubing. A check after another eight hours showed fifty percent remaining in the tubing. During the following week random inspections showed the percentage to range from twenty-five to seventy-five percent of the animals remaining within the artificial tubes.

Holmes (1901a) felt that thigmotaxis was basic to many innate behavioral patterns. He stated:

> If the origin of the various forms of amphipod behavior could be traced, it would be found, I believe, that thigmotaxis is the mother of many instincts.

Since these origins cannot be traced, it is merely speculation that thigmotaxis is basic to other behavior patterns. How does one explain innate behaviors such as feeding, removal of wastes as accomplished by this species, swimming, moulting and even reversal within the nest? The latter may be related to the point that Holmes makes but it is stretching the issue. Coupled with this, it would not explain the other tactic behaviors displayed by this animal. It is true, however, that thigmotaxis is basic to much of the nesting behavior of this species.

A. valida displays a strong negative phototaxis. In nature it will seek out the dark areas if disturbed or captured and subsquently released. This is possibly a combination of negative phototaxis and positive geotaxis. The animal will not only swim down to the dark areas, but will swim laterally towards a darkened area. The resultant

direction is some angle between entirely horizontal and entirely vertical.

In the laboratory it was a simple matter to test this tactic behavior. Groups of animals were placed in a white tray which was blackened for one half of its area. A cluster of Ulva was placed at each end to afford food and shelter. The animals were then introduced in the center of the tray at the dividing line between the light and dark zones. Once released, a lamp was turned on and periodic inspections were made to determine the numbers of animals in either zone.

In two experiments involving a total of 32 animals of both sexes and various states of maturity, the response to light can be said to be negative. The percentage of individuals found in the darkened zone after twenty-four hours was ninety-four. After thirty-six hours, the percentage was 100. At this time the animals were removed from the Ulva and the positions of the Ulva were reversed. The animals were then again introduced. The twenty-four hour inspection revealed seventy-three percent of the individuals in the dark zone. At thirty-six hours the percentage was ninety. These percentages do not include mortalities and are based on living animals only at the time of inspections. No attempt was made to test the effect of varying the salinity or temperature. The temperature was $22^{o}C \pm 1^{o}C$ and the salinity was $24^{o}/_{oo} \pm 1^{o}/_{oo}$. It is possible that a change in temperature or salinity might

affect this behavior. However, Holmes (1901a) reported only negative results in attempting such experiments with A. longimana and other aquatic amphipods (1901b).

As was indicated previously, this species is positively geotactic and will swim down to the Ulva or substrate. This is not merely a consequence of its having a higher specific gravity than the water. It has been observed to make a direct path in its swimming both in its natural habitat and in the laboratory. In the laboratory this was demonstrated by placing Ulva at the surface of a tall beaker filled with sea-water and then releasing the animals. Their first reaction was a straight swim to the bottom. After this, they began aimless swimming, and some eventually found the Ulva at the surface. A second observation concerning their habits in culture, which indicated a positive geotactic behavior, was that the animal would crawl under the Ulva to build its tube. Once the tube had been built, the animal would leave it to build another if the Ulva was turned over to place the animal on the top. It did not matter what direction the light came from. Transmitted light of high intensity could be focused from below the animal and it would still crawl under the Ulva.

Experiments and observations were made concerning any rheotactic behavior on the part of this species. These observations and data were taken for fifty individuals. They showed the species to be highly rheotactic. The

animals will attempt to swim against a current which is strong enough to carry them with it. All fifty animals reacted positively to the current. They possess enough speed and agility in swimming to avoid capture by a suction pipette. As soon as they have been sucked into the pipette, and on occasions even before, they orient themselves to face the direction of flow and swim away. Each animal was tested in the pipette for a reaction three times. Six of the fifty did not react for two of the three attempts. However, all of these six did react at least once.

Food and Feeding. This species has shown itself to be an omnivorous feeder with what seems to be an insatiable appetite. In the natural habitat Ulva is the major source of food. Laboratory studies have shown, however, that given the opportunity to change its diet, the animal does so readily. From these observations, it seems unlikely that the animal would reject a change in its diet in the field if the chance arose.

A. valida has never been observed in culture or in the field to act as a predator other than to occasionally attack a dying or injured animal. One other exception is discussed under cannibalism. Faunal associates such as Anomia, Botryllus, Microdeutopus, Mytilis spat, ectoprocts, hydroids, various calanoid copepods and various other gammarids are not attacked while they are alive. In culture, these various faunal associates were left unharmed until they were crushed or destroyed in some other manner. Once

destroyed, A. valida attacked the carcass and began voraciously feeding upon them. The hydroids were investigated but rejected.

In culture, foods which are not in the realm of the natural environment were offered. Some were readily accepted and eaten. Others were accepted, chewed on and then rejected. The outside foods were lettuce, tomato, potato, apple, bread, raw and cooked beef and raw and cooked bacon. The lettuce, bacon and beef were accepted and readily eaten. The bread was accepted but became soft and soon fell to pieces, thereby being lost to the animal.

Plants and animals which live in the natural environment but not usually associated with A. valida were offered and found to be acceptable as long as there was soft tissue accessible to the animal. Some of those tested were Fundulus, Nereis, Mya arenaria, Mytilis edulis, Homarus americanus, Cancer borealis, C. irroratus, Ascophyllum, Fucus and various other algae. The algae proved to be the least acceptable. This was accepted, tested and then rejected.

Cannibalism exists within the species but usually occurs only after the death of the victim by some other cause. Occasionally a weakened individual will be attacked and eaten. This usually occurs during the final stages of moulting.

Coprophagy was witnessed on numerous occasions. It is believed that due to the nature of the fecal material,

this is one of the primary sources of food for the brooding immatures. The fecal material has a characteristic green color which is as brilliant as the Ulva, the original source. As previously described, the abdomen is moved anteriorly to such a position so as to allow the gnathopods and mouthparts to take a hold on the fecal pellet. At this time, the brooding young reach out from the brood pouch and grasp the fecal material, whereupon they feed upon it. Once the immatures begin leaving the brood pouch, they can usually be found building their tubes near or in fresh fecal material.

Feeding is accomplished by the use of mouthparts, and on occasions, both pairs of gnathopods. The glandular pereiopods usually secure the food to the tube. The movement of the mouthparts is rather slow and deliberate and not as rapid as indicated for other species by Kunkle (1918). The rate of mandibular movement for A. valida is a maximum of seventy bites per minute. When the animal becomes aware of a source of food outside the tube, it quickly darts out of the tube just far enough to grasp the food with its gnathopods and then just as rapidly retreats back into the tube with its food. As soon as the item has been grasped, the glandular pereiopods begin attaching it to the tube. As the item is being loosely attached, the mandibles are biting off small bits to be ingested. They were never observed to use the gnathopods to tear off small portions first. This is in agreement with A. longimana

(Holmes 1901a). In feeding on the Ulva surrounding the tube, A. valida reaches out from its tube by extending itself as far as possible. As it slowly retreats back into the tube it begins to flex its body and takes a series of bites along the edge of the Ulva. This procedure is repeated several times. The resulting design of the eaten out area of Ulva is circular.

SECTION VI

MOULTING AND GROWTH

The phenomenon of ecdysis is characteristic for all arthropods. It occurs rather periodically and is the manner by which growth is allowed to occur. The process of moulting has been described by Sexton (1924) for Gammarus chevreuxi Sexton and for G. fasciatus Say by Clemens (1950). These descriptions of moulting compare favorably with that observed for A. valida.

The process begins with a transverse separation in the cuticle between the cephalon and the pereion (Figure VI-1). This separation is followed by longitudinal separations between the dorsal plates and coxal plates. These separations extend posteriorly for about three to five segments. Once these splits have been completed, the animal has enough room to exit the exuvium. This is accomplished by pulling the cephalon and associated structures dorsally and posteriorly while the gnathopods retain a hold on the exuvia. The lining of the stomodaeum is shed in this movement (Figure VI-2). The amphipod then repeatedly reflexes its abdomen anteriorly such that the uropods come in contact with the gnathopods. These appendages usually grasp the urosome and hold it in place. The abdomen is then extended to the posterior. This action pulls the body out of the posterior portions of the exuvium.

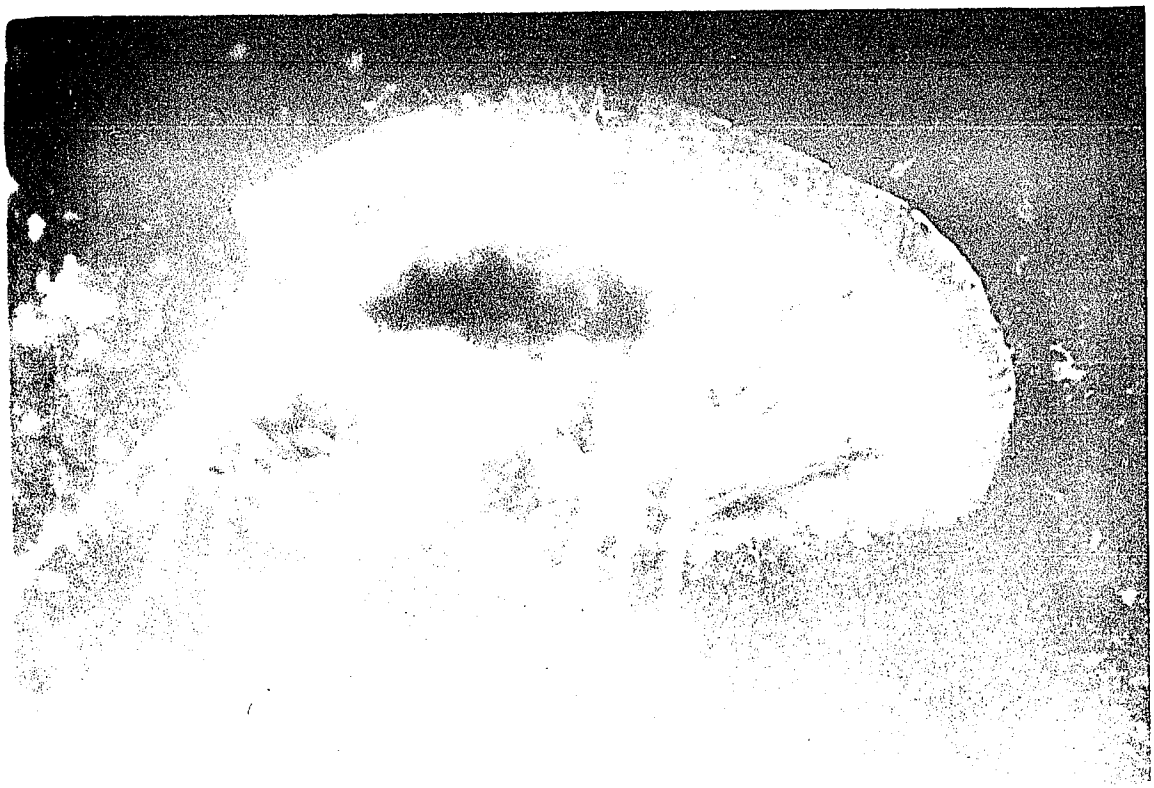

Figure VI-2. Photograph showing the locations of the transverse split and the longitudinal splits involved in the moulting process.

When this occurs, the proctodaeum is then shed (Figure VI-3). The exuvia of the appendages are the last to be shed. This is accomplished by rapid and vigorous movements which appear to literally wash the remaining exuvia away. The exuvium is usually shed in its entirety. Males possessing large second gnathopods exhibit some difficulty in shedding the exuvium of the propodus and may carry this part somewhere else and shed it at a later time. On occasions it was observed that partial moulting occured, wherein portions of the antennae, cephalon and urosome were not shed. In the case of the cephalon not being shed, the individual died within two days. It is suspected that this individual starved to death.

Prior to moulting, the amphipods become quiescent and do not feed. They typically assume a much withdrawn position. The pleopod beat is reduced and they do not assume the alert position unless violently disturbed. In most cases, A. valida will leave its tube just prior to moulting and will moult outside the tube. This agrees with Holmes' statement concerning A. longimana:

> In the several cases in which I observed the process, Amphithoe leaves its nest to divest itself of its skin, and I have never observed a moult in a nest but always some distance away.

However, this phenomenon of moulting within the nest has been observed in culture for five different individuals. Three of these individuals were immatures.

In view of the habitat at Great Bay Marina and no doubt other similar habitats, it would seem unlikely that

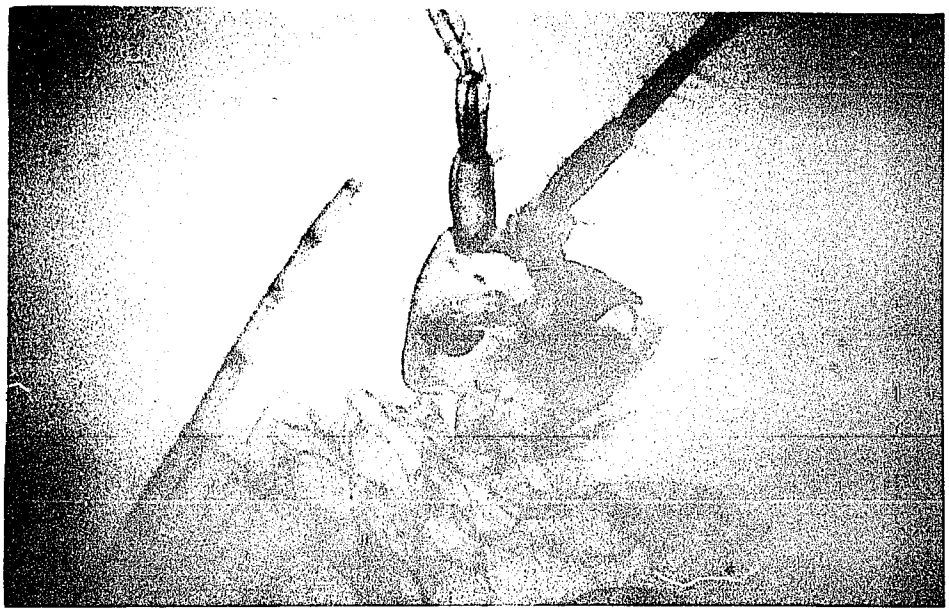

Figure VI-2. Photograph showing the stomodeal lining which is shed.

Figure VI-3. Photograph showing the proctodeal lining which is shed (note the fecal material present in the proctodaeum).

crawling out of the tube would be a survival trait. Leaving the tube would subject the animal to increased predation especially in view of the weakened condition of the animal after moulting. It would also mean, in most cases, a swim back up from the substrate to the Ulva. This again would prove to be hazardous. In culture or in intertidal and benthic beds of Ulva, this would not be so vital to the maintainance of the species.

After moulting, the amphipod appears to be weak and un-co-ordinated. It makes rapid but feeble movements at first which accomplish no apparent ends. Within three to five minutes, it begins to swim in short spurts and crawl a little. Within one half hour, the amphipod appears to be able to function normally.

It is during the process of moulting that the greatest mortality occurs. This mortality during moulting is, by far, most prevalent in immatures. What the actual cause for death in these immatures is, has not been discovered. One cause, in culture, for both adults and immatures alike is predation and cannibalism. This is rather rare. This occurs when a moulting individual moults near the tube of another non-moulting individual. Holmes (1901a) made note of the high mortality during the moult process but offered no explanation. He also mentions observing the exuvia floating on the surface of the water. This has never been observed for the exuvia of A. valida.

The exuvium is usually left untouched by the adults but occasionally they may eat a part of it. The immatures are more prone to eat the exuvium or at least some portion of it.

Moulting in adults does not appear to follow a predictable time pattern. Brooding females will usually moult after the release of all the immatures. This is the only predictability noted in the observations regarding adult moulting.

Immatures are fairly predictable in the lengths of the intermoult. A study of the periodicity of moulting in immatures from the time they leave the brood pouch until they reach maturity was made. This study was carried out on individuals maintained at room temperature (21°C + 10° -1°) and 12°C ± 1°C (Figure VI-4 and VI-5). The individuals were isolated and supplied with sufficient Ulva to feed and shelter them. The immatures used were from two different females collected at Nannie Island and Great Bay Marina.

A comparison of figures VI-4 and VI-5 reveals that the length of the intermoult period for cultures maintained at room temperatures is less than that of cultures maintained at 12°C ± 1°. The intermoult period of individuals maintained at room temperature increased rather steadily from one moult to the next. The intermoult periods following maturation increased rapidly and soon lost all predictability. The individuals maintained at 12°C ± 1°, with the exception of the first two moults, showed a

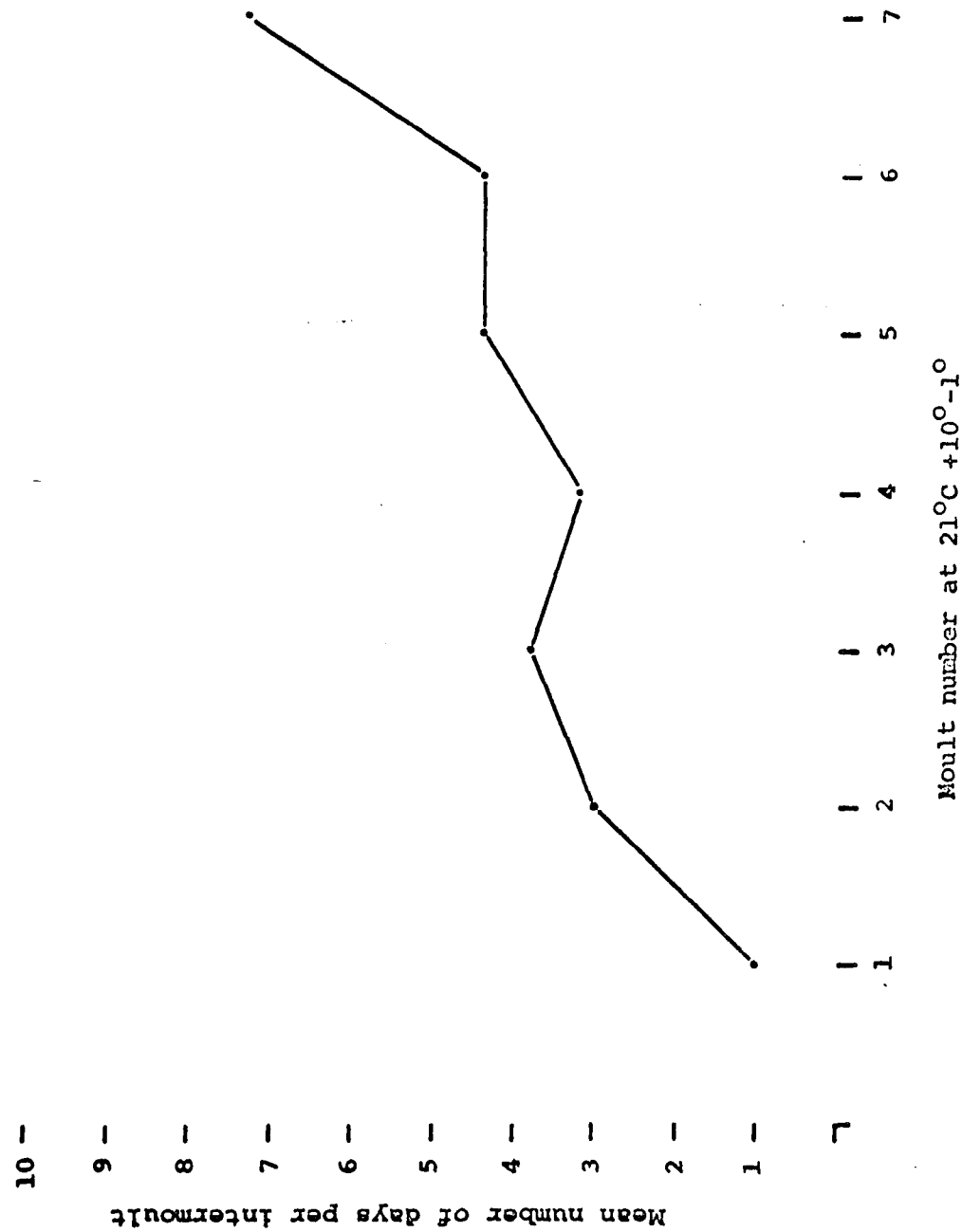

Figure VI-4. Relationship of the mean number of days per intermoult and the moult number at 21°C +10° -1°.

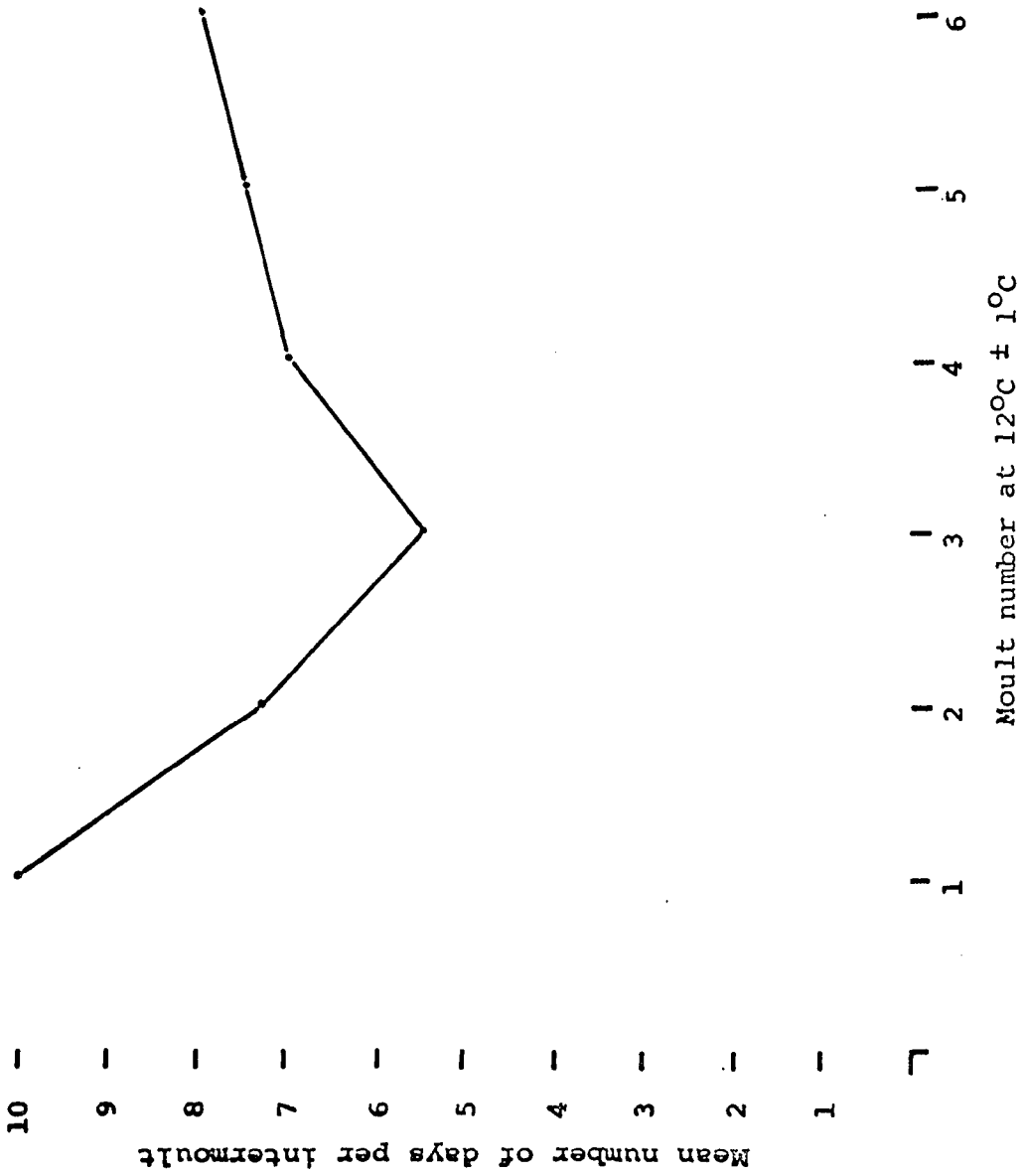

Figure VI-5. Relationship of the mean number of days per intermoult and the moult number at 12°C ± 1°.

similar increase in length of intermoult. It is not known exactly why the first two intermoult periods in these individuals required so much time. It is known that during these two moults, the mortality rate is higher than during the rest of the moults.

As mentioned previously, mortality in immatures is high. This problem reduced the number of immatures in this study from twenty at the beginning to five at the end of the study. Therefore, the results shown in this section are based on these five individuals.

Measurements were taken on the exuvia at each moult for total body length, cephalon length, antenna I length and number of articles, antenna II length and number of articles, peduncular segments one, two and three for antenna I, peduncular segments four and five for antenna II and the lengths of the basis, endopodite and exopodite for uropods I, II, and III. These morphological regions were chosen for ease of measurement and what appeared to be regions which showed the least variation between individuals.

Measurements on total body length of immatures cultured at room temperature ($21^{\circ}C + 10^{\circ} -1^{\circ}$) just prior to hatching and taken from the egg, showed them to measure 1.4 millimeters $\pm$ 0.05 millimeters in length. The first antenna of these immatures possessed four flagellar articles and the second antennae possessed three flagellar articles. Within twenty-four hours after hatching, immatures measured 1.6 millimeters $\pm$ 0.02 millimeters. The number of flagellar

articles remained the same as before hatching. Upon leaving the brood pouch, the immatures measured 1.9 millimeters ± 0.02 millimeters. The number of articles for both antennae remained the same as previously mentioned (Table VI-1). Immatures cultured at 12°C ± 1° measured 1.9 millimeters ± 0.05 millimeters upon leaving the brood pouch and measured 2.2 millimeters ± 0.05 millimeters at the onset of the first moult. In these individuals the flagellar counts were the same as for those reared at room temperature.

Sixteen immatures taken from the brood pouch of A. rubricata averaged 2.38 millimeters in length. The standard deviation was 0.05 millimeters. The articular counts for the flagella of the two antennae were the same as shown for A. valida.

From these evidences, it is clearly seen that growth does occur during the brooding period. In no instances were exuviae found in the brood pouches of the females or in the dishes prior to the exit of the immatures. This fact, in conjunction with the constant number of flagellar articles, makes it fairly apparent that the immatures do not moult while they are brooding. The total percent growth during brooding is consistent with those percentages for intermoult growth. It was not observed in this study if moulting ocurred within the eggs as Clemens (1950) reported that Roux (1933) had observed in Gammarus duebeni (now Rivulogammarus duebeni, Barnard, 1958).

TABLE VI-1

Comparisons of brooding immatures

	Prior to hatching	24 hours after hatching	Prior to first moult
Body length in millimeters	1.4	1.6	1.9
Number of flagellar articles Antenna I	4	4	4
Number of flagellar articles Antenna II	3	3	3

TABLE VI-2

Mean body length per moult at 21°C +10 -1

Intermoult	Moult	Mean increase mm.	% Increase	Mean length at moult mm.
	1			1.9
I		.5	26	
	2			2.4
II		1.0	41	
	3			3.4
III		1.0	30	
	4			4.4
IV		1.0	30	
	5			5.7
V		1.3	22	
	6			7.0
VI		1.2	17	
	7			8.2

The rate of growth and brooding for immatures from the time they hatch until the time they leave the brood pouch has been discussed. The remainder of the findings and discussion will concern the rate of growth of the immatures from the time they leave the brood pouch until they attain sexual maturity. This includes the first six moults and the corresponding intermoults. Percent growth was determined for each intermoult and was based on the mean body length of the animals at the preceeding moult divided into the mean body length of the current moult. This value was multiplied by 100. The difference between this value and 100 represents the percent growth during the intermoult period just concluded.

Immatures raised in culture at $21^{\circ}C$ $+10^{\circ}$ -1° had a mean percent growth per moult of 27.6%. The range was from 17% to 41% (Table VI-2). The percent growth increases to the second intermoult period and slowly decreases with each succeeding intermoult. Upon reaching the sixth moult, the percent growth declines to approximately 56% of the mean of the preceding five moults. In the few observations taken on adults, it appears that this growth percentage decreases even more.

When immatures raised in culture at $12^{\circ}C$ $\pm 1^{\circ}$ began the seventh moult they averaged 8.7 millimeters in length. Those raised at $21^{\circ}C$ $+10^{\circ}$ -1° averaged 8.2 millimeters in length. As previously mentioned in section II, the food and crowding conditions were optimal. In the natural

habitat it would seem unlikely that these individuals would grow quite as fast.

Immatures raised in culture at 12°C ± 1° compared quite favorably with the warmer cultures in the percent growth. The mean percent growth was 26% with a range of 16% to 32%. Here again, the last intermoult period showed a decrease to 57% of the mean of the five preceeding intermoults (Table VI-3).

In females, the sixth intermoult period is denoted by the development of the gonads. This activity is plainly noticable and could possibly explain the sharp decline in body length growth. Although the gonads of the male are not visible to the naked eye, the same would be expected for them.

The number of articles of the flagella of the two pairs of antennae does not increase steadily with each moult (Table VI-4). However, as shown by the tables in appendix B, a heterogonic growth relationship does exist between the lengths of the flagellum and the various peduncular segments. This relationship is not so apparent with regards the flagellum of the second antenna and its peduncular segments.

TABLE VI-3

Mean body length per moult at 12°C ± 1

Intermoult	Moult	Mean increase mm.	% Increase	Mean length at moult mm.
	1			2.2
I		.7	32	
	2			2.9
II		.9	31	
	3			3.8
III		.8	21	
	4			4.6
IV		1.3	28	
	5			5.9
V		1.6	27	
	6			7.5
VI		1.2	16	
	7			8.7

TABLE VI-4

Relationship of flagellar articles to moult

Moult	Number of articles Antenna I	S_x	Number of articles Antenna II	S_x
1	4	0	3	0
2	5	0	3	0
3	9	1	5	1
4	12	1	7	1
5	14	1	9	2
6	18	1	11	.5

SECTION VII

DISTRIBUTION AND HABITAT

General. The known geographic distribution of A. valida to this date is the east coast of the United States, the west coast of the United States and possibly Japan. The current literature lists the type locality as Beesley's Point, New Jersey. Nagle (unpublished) reports a population from Barnstable Harbor, Cape Cod, Massachusetts. This locates the species north of the Cape and into the colder waters of the Gulf of Maine.

In July, 1962, the species was collected in an estuarine habitat in New Hampshire. The importance of this collection was not recognized at that time and no further collections were made until May, 1965. The 1962 collection was the result of the efforts of a group of students enrolled in an invertebrate natural history course at the University of New Hampshire.

Currently, Dr. E. L. Bousefield, in conjunction with the Systematics and Ecology Program at the Woods Hole Marine Biological Laboratories, is working on the distribution of this species and others in the Cape Cod region. At this time no publications have been made to indicate the distribution of A. valida in this region.

As previously indicated, the species has been reported twice on the west coast of the United States. The specimens discussed by Barnard have been compared with

those of the east coast and do compare favorably.

Local Distribution. The specimens involved in this study were collected from seven localities along the east coast of the United States. Six of these seven localities were in Little Bay and Great Bay complex (Figure VII-1). The seventh collection site was Milford Harbor, Milford, Connecticut. This site was the southern most point visited. The animals were taken from the Ulva growing on timbers supporting trays at the lower intertidal level at the U. S. Bureau of Commercial Fisheries Laboratory, Milford, Connecticut. The northern most site for collection was Emerson's Beach, Little Bay, Durham, New Hampshire (N 43° 7' 50"; W 70° 52' 10"). A. valida was located at and collected at the Great Bay Marina, Newington, New Hampshire (N 43° 7' 30"; W 70° 50' 00"); Fox Point, Newington, New Hampshire (N 43° 7' 40"; W 70° 52' 00"); Goat Island, Newington, New Hampshire (N 43° 7' 45"; W 70° 51' 50"); Adams Point, Durham, New Hampshire (N 43° 5' 40"; W 70° 52' 10"); Footman Islands, Durham, New Hampshire (N 43° 5' 20"; W 70° 52' 30") and Nannie Island, Newington, New Hampshire (N 43° 4' 10"; W 70° 52' 5").

Ulva beds have been examined at Reid State Park, Maine; Bailey's Mistake , Maine and Moosehorn Reservation, Maine. The results of these collections and examinations proved to be negative. Beds of Ulva found subtidally along the coast of New Hampshire were examined for the presence of A. valida. None were found. Examinations of

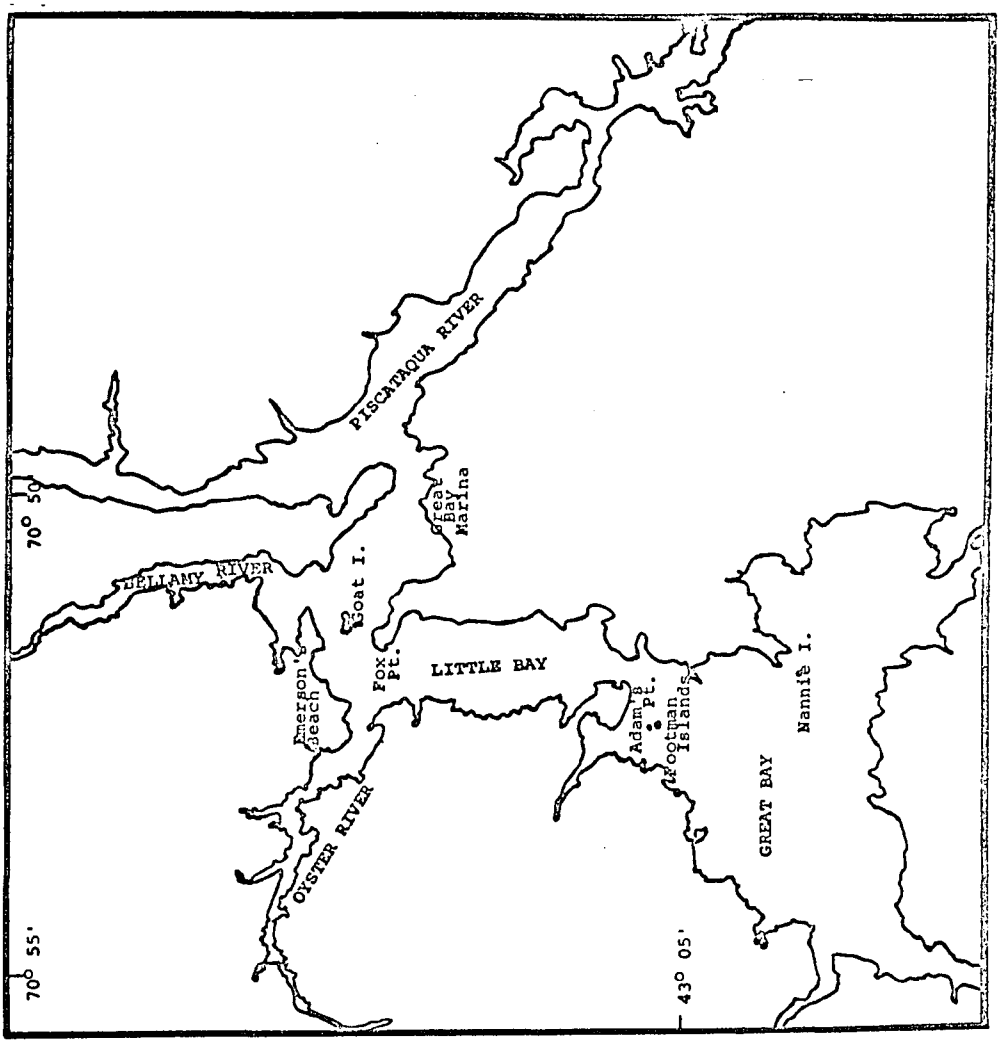

Figure VII-1. Map of the Piscataqua River and the Great Bay complex. (Taken from: United States Dept. of the Army, Corps of Engineers, Dover Quadrangle-Topographic Map).

Ulva taken from the tidal creeks of Hampton River, New Hampshire, Sagamore Creek, Portsmouth, New Hampshire and the Oyster River at Jackson's Landing, Durham, New Hampshire revealed no populations of A. valida existing in these areas.

At the present time, this study extends the known geographic range of A. valida approximately 170 statute miles due north of the type locality and 95 statute miles due north of Cape Cod, Massachusetts.

General Habitat. A. valida in this region is typically a brackish water and estuarine animal. It lives in the intertidal to subtidal regions which are suitable sites for Ulva. The salinity range at which the Little Bay and Great Bay populations lived was $18^{o}/_{oo}$ to $31^{o}/_{oo}$. The denser populations were found in areas where the salinity rarely exceeded $26^{o}/_{oo}$ or fell below $20^{o}/_{oo}$. The water temperatures during the summer months ranged from $18^{o}C$ to $24^{o}C$. The spring and fall temperature fell to $6^{o}C$ and the winter temperatures fell to $-1.8^{o}C$. At the winter temperatures, the bays freeze over and the intertidal populations disappear.

The habitat of the population sampled at the Great Bay Marina was Ulva which grows on the floats. Due to the nature of the tidal currents and the salinity, this area does not freeze over solidly. However, the population of A. valida left the accessible portion of this area by December. Likewise, the intertidal areas of Adam's Point,

Fox Point, Nannie Island and Emerson Beach have all become devoid of their populations. Subtidal samplings in late November and early December at these various areas show a small population remaining. The majority of the individuals in these samples were immatures. Some adult females were collected, but none were found to be ovigerous.

It is believed that this is approximating the northernmost limit of the range for the species. On this premise, the habits, habitat preference and life history of this species may be expected to be somewhat different from those of the more southern regions occupied by this species.

Specimens of the Great Bay and Little Bay complex will be deposited at the U. S. National Museum, Washington, D. C., Peabody Museum of Natural History, Yale University, New Haven, Connecticut, and at the Allan Hancock Foundation, University of Southern California, Los Angeles, California.

SECTION VIII

SUMMARY

The taxonomic status, morphology, description and general natural history of the gammaridean amphipod, Ampithoe valida Smith is presented in this thesis. Included also is a general description of the habitat and an extension of the known geographic range for this species.

Since 1873, when Smith first described the species from New Jersey and Long Island Sound, very little has been written about the species. The literature to date involves merely describing the male and ignoring the female or acknowledging that there is some confusion as to its identity. The present study went into a fair amount of detail and presents a description of the female including seven one millimeter size classes ranging from the eight millimeter size class to the fourteen millimeter size class. Where it was deemed necessary, information was added to the recent description of the male (Mills, 1964). A brief account was given with regards the immatures of this species.

A. valida was compared with the two most common ampithoids found along the east coast of the United States and distinctions between these species were pointed out. The Great Bay specimens were compared with those specimens collected in Oregon and deposited at the Allan Hancock Foundation. The results of these comparisons are not

entirely conclusive, but at this time, it is believed that the two populations are of the same species.

A. shimizuensis Steph. is taken out of the synonomy of A. valida primarily because of differences found in the first gnathopods of both sexes, the fourth peduncular segment of the second antennae, the spination of the peduncle of the first uropod and the shape of the telson.

Investigations into the tactic behavior, feeding, movements and tube building were carried out. A. valida is negatively phototactic. It is positively rheotactic, geotactic and thigmotactic. There is some indication that the thigmotactic reaction is increased during the time the female is brooding eggs or young. The tubes are constructed within the basal folds of Ulva and do not incorporate foreign materials. They are open at both ends and the animal is somewhat loath to leave them.

Observations and experimentation pointed out that copulation must occur prior to ovulation to ensure viable offspring. It is apparent that the female does not store sperm from one mating to fertilize further broods of eggs. Unlike what Holmes (1901a) stated for A. longimana, the male does not pair with and carry the female prior to copulation. The individuals live separately except for the short time that the female is receptive to the male's advances.

Brooding times were recorded for several females. These records included the time of copulation (when observed), ovulation, hatching and the time of exit of the

immatures. Egg counts were taken and recorded against the total body length of the female. The results of this showed that the numbers of eggs per brood were dependent upon the size of the female. The size of the brood, in terms of numbers of eggs, did not have a significant effect upon the time required to hatch. Temperature did, however, have an effect upon the hatching time. A similar study was carried out with reference to the numbers of immatures per female size. The results were the same.

Moulting and growth were investigated during this study. The process of moulting is described for both the adult and the immature. Growth studies were primarily concerned with the immatures. The results led to the conclusion that there was a definite size increase during brooding but that there were no moults during this time. A comparison of the immature just prior to hatching, to just after hatching and just after leaving the brood pouch is included. The immatures moulted at fairly predictable intervals. Sexual maturity was attained between the sixth and seventh moults. Ovulation of the first brood occurred after the seventh moult.

A. valida is rather abundant in Great Bay, N. H. It can be found at almost every site that Ulva can be located. Investigations into other tidal river systems and estuaries along the north east coast has not shown them to be existent in these areas. At the present time, the species is known north of Cape Cod, Massachusetts only

from Barnstable Harbor, Massachusetts and Great Bay, New Hampshire.

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Key to Symbols Used in Tables A-1, B-1, 2, 3 and C-1

Bas, Basal segment
Car, Carpal segment
Cox, Coxal plate
Dac, Dactyl
En, Endopodite
Ex, Exopodite
F, Flagellum
Gn I, First gnathopod
Gn II, Second gnathopod
IAL, Interantennal lobe
Isch, Ischial segment
L, Length
Lat, Lateral
max, Maximum
Med, Medial
Mer, Meral segment
Md, Mandible
min, Minimum
Mx I, First maxillae
Mx II, Second maxillae
Mxpd, Maxilliped
P_1, First peduncular segment of antennae
P_2, Second peduncular segment of antennae
P_3, Third peduncular segment of antennae
P_4, Fourth peduncular segment of antennae
P_5, Fifth peduncular segment of antennae
Pal, Palm
Ped, Peduncle of Uropod
Per I, First pereiopod
Per II, Second pereiopod
Per III, Third pereiopod
Per IV, Fourth pereiopod
Per V, Fifth pereiopod
Post, Posterior
Pro, Propodal segment
S_1, Basal segment

S_2, Second segment distally

S_3, Third segment distally

set, Setae
spn, Spines

Uro I, First uropod
Uro II, Second uropod
Uro III, Third uropod

APPENDIX A

Table A-1. Means of measurements taken on adult females of Ampithoe valida Smith for seven different size classes.

Table A-1. Mean Measurements In Millimeters

mm. Size Class	Eye L	Eye W	IAL L	IAL W	Md palp S_1 L	Md palp S_1 W	Md palp S_2 L	Md palp S_2 W	Md palp S_3 L	Md palp S_3 W
8	.22	.18	.13	.39	.08	.04	.18	.07	.20	.07
9	.28	.20	.14	.40	.09	.06	.20	.08	.22	.09
10	.26	.20	.15	.43	.10	.06	.21	.08	.23	.08
11	.28	.20	.16	.47	.11	.07	.23	.10	.27	.10
12	.30	.22	.19	.56	.12	.08	.27	.11	.29	.11
13	.31	.25	.19	.62	.13	.09	.27	.11	.29	.12
14	.34	.27	.21	.74	.14	.08	.32	.13	.34	.14

	Mx I palp S_1 L	Mx I palp S_2 L	Mx I palp S_2 W	Mxpd palp S_1 L	Mxpd palp S_1 W	Mxpd palp S_2 L	Mxpd palp S_2 W	Mxpd palp S_3 L	Mxpd palp S_3 W
8	.07	.22	.07	.17	.12	.19	.13	.15	.10
9	.08	.24	.08	.20	.14	.22	.14	.16	.11
10	.08	.25	.09	.21	.15	.24	.16	.17	.13
11	.10	.29	.10	.24	.16	.26	.16	.19	.14
12	.10	.32	.10	.26	.18	.31	.18	.20	.15
13	.11	.32	.11	.27	.18	.31	.18	.20	.14
14	.11	.36	.13	.32	.22	.38	.22	.25	.17

Table A-1. Mean Measurements In Millimeters

mm. Size Class	Antenna I FL	P_1L	P_2L	P_3L	Antenna II FL	P_3L	P_4L	P_5L
8	2.3	.53	.45	.18	1.2	.20	.60	.55
9	3.0	.61	.53	.23	1.5	.24	.71	.64
10	3.3	.63	.58	.24	1.4	.26	.77	.71
11	4.2	.79	.68	.27	2.2	.29	.90	.84
12	4.4	.80	.75	.30	2.6	.32	1.00	.95
13	4.0	.82	.77	.31	2.2	.33	.97	.90
14	4.6	.97	.87	.34	2.9	.39	1.10	.99

	Uropod I Ped L	Ex L	En L	Uropod II Ped L	Ex L	En L
8	.65	.35	.39	.43	.27	.34
9	.72	.41	.46	.48	.30	.37
10	.80	.43	.48	.55	.33	.39
11	.91	.51	.54	.61	.39	.46
12	1.00	.60	.65	.70	.45	.52
13	1.00	.59	.67	.72	.46	.55
14	1.20	.75	.81	.85	.55	.66

Table A-1. Mean Measurements In Millimeters

mm. Size Class	Uropod III Ped L	Ex L	En L
8	.30	.13	.16
9	.35	.16	.19
10	.39	.16	.19
11	.44	.18	.21
12	.49	.22	.25
13	.50	.21	.25
14	.61	.25	.30

	Telson L	W
8	.21	.28
9	.23	.31
10	.24	.32
11	.25	.34
12	.30	.39
13	.33	.42
14	.35	.46

Table A-1. Mean Measurements In Millimeters

mm. Size Class	Gnathopod I Dac L	Pro L	Pro W	Pal L	Car L	Car W	Mer L	Mer W
8	.29	.52	.27	.27	.42	.27	.27	.17
9	.32	.56	.28	.30	.45	.28	.30	.16
10	.35	.60	.32	.33	.51	.32	.32	.19
11	.39	.68	.35	.36	.57	.35	.36	.19
12	.44	.74	.40	.41	.63	.39	.41	.23
13	.48	.77	.40	.45	.67	.41	.43	.24
14	.54	.93	.46	.49	.79	.45	.49	.26

	Gnathopod I Isch L	Isch W	Bas L	Bas W	Cox L	Cox W
8	.21	.16	.67	.24	.72	.67
9	.23	.18	.73	.26	.81	.71
10	.24	.19	.81	.27	.92	.78
11	.29	.19	.91	.30	.97	.87
12	.33	.23	1.10	.34	1.10	.99
13	.34	.24	1.10	.37	1.10	1.00
14	.34	.26	1.20	.40	1.30	1.10

Table A-1. Mean Measurements In Millimeters

mm. Size Class	Gnathopod II Dac L	Pro L	Pro W	Pal L	Car L	Car W	Mer L	Mer W
8	.30	.54	.32	.28	.32	.31	.32	.16
9	.33	.58	.34	.31	.33	.33	.34	.18
10	.32	.63	.37	.32	.38	.36	.36	.19
11	.40	.70	.41	.37	.40	.39	.40	.20
12	.43	.77	.47	.41	.48	.47	.48	.25
13	.46	.80	.48	.43	.48	.47	.50	.26
14	.54	.90	.53	.51	.56	.54	.56	.25

	Gnathopod II Isch L	Isch W	Bas L	Bas W	Cox L	Cox W
8	.23	.18	.71	.32	.75	.54
9	.24	.20	.81	.34	.86	.60
10	.27	.22	.89	.38	.97	.66
11	.29	.25	.99	.40	1.00	.75
12	.35	.28	1.20	.47	1.20	.87
13	.34	.27	1.20	.48	1.30	.89
14	.38	.30	1.40	.55	1.50	.99

Table A-1. Mean Measurements In Millimeters

mm. Size Class	Pereiopod I Pro L	Pro W	Car L	Car W	Mer L	Mer W
8	.37	.10	.35	.13	.33	.21
9	.40	.10	.39	.13	.39	.21
10	.43	.13	.42	.16	.42	.24
11	.50	.14	.49	.17	.47	.25
12	.55	.14	.55	.19	.55	.29
13	.56	.15	.55	.19	.55	.29
14	.66	.15	.64	.20	.65	.32

	Pereiopod I Isch L	Isch W	Bas L	Bas W	Cox L	Cox W
8	.22	.18	.87	.39	.83	.59
9	.24	.18	1.00	.39	.96	.69
10	.26	.20	1.10	.45	1.10	.77
11	.31	.22	1.30	.49	1.20	.86
12	.34	.24	1.40	.54	1.40	.96
13	.35	.24	1.40	.53	1.50	1.00
14	.35	.26	1.70	.59	1.70	1.20

Table A-1. Mean Measurements In Millimeters

mm. Size Class	Pereiopod II Pro L	Pro W	Car L	Car W	Mer L	Mer W
8	.36	.10	.33	.13	.32	.21
9	.39	.10	.38	.14	.37	.21
10	.42	.12	.41	.15	.40	.24
11	.49	.14	.49	.17	.46	.27
12	.54	.15	.53	.19	.52	.30
13	.55	.15	.55	.19	.54	.30
14	.64	.16	.65	.20	.64	.33

	Pereiopod II Isch L	Isch W	Bas L	Bas W	Cox L	Cox W
8	.23	.17	.86	.38	.88	.66
9	.22	.18	.98	.39	1.00	.76
10	.27	.19	1.10	.46	1.10	.84
11	.30	.23	1.20	.50	1.30	.93
12	.33	.24	1.40	.54	1.50	1.10
13	.33	.24	1.50	.55	1.60	1.10
14	.35	.25	1.80	.64	1.70	1.20

Table A-1. Mean Measurements In Millimeters

mm. Size Class	Pereiopod III Pro L	Pro W	Car L	Car W	Mer L	Mer W
8	.45	.14	.31	.19	.38	.23
9	.47	.15	.33	.20	.42	.24
10	.52	.17	.36	.21	.46	.28
11	.57	.19	.44	.23	.55	.29
12	.63	.21	.47	.27	.61	.34
13	.63	.22	.51	.27	.63	.34
14	.77	.25	.57	.29	.77	.38

	Pereiopod III Isch L	Isch W	Bas L	Bas W	Cox L	Cox W max	Cox W min
8	.21	.20	.71	.67	.92	.93	.72
9	.22	.22	.77	.76	1.10	1.10	.86
10	.25	.25	.86	.86	1.20	1.20	.95
11	.27	.28	1.00	.95	1.40	1.40	1.10
12	.32	.30	1.10	1.00	1.60	1.50	1.30
13	.31	.31	1.10	1.10	1.70	1.60	1.30
14	.33	.35	1.30	1.20	1.80	1.70	1.40

Table A-1. Mean Measurements In Millimeters

mm. Size Class	Pereiopod IV Pro L	Pro W	Car L	Car W	Mer L	Mer W
8	.59	.15	.41	.17	.51	.21
9	.65	.16	.44	.17	.55	.21
10	.71	.18	.49	.19	.63	.25
11	.78	.19	.55	.23	.72	.27
12	.84	.20	.63	.25	.83	.31
13	.82	.22	.63	.24	.82	.30
14	1.00	.24	.71	.28	.94	.34

	Pereiopod IV Isch L	Isch W	Bas L	Bas W	Cox L	Cox W
8	.23	.20	.77	.52	.33	.52
9	.24	.21	.85	.57	.35	.56
10	.28	.24	.97	.62	.39	.62
11	.30	.27	1.10	.72	.45	.71
12	.34	.30	1.20	.81	.53	.80
13	.34	.31	1.20	.78	.56	.79
14	.36	.33	1.40	.92	.66	.91

Table A-1. Mean Measurements In Millimeters

mm. Size Class	Pereiopod V Pro L	Pro W	Car L	Car W	Mer L	Mer W
8	.63	.15	.42	.16	.53	.19
9	.69	.16	.50	.17	.63	.20
10	.76	.18	.54	.20	.70	.24
11	.86	.20	.60	.22	.81	.25
12	.92	.22	.71	.24	.90	.28
13	.94	.22	.70	.25	.92	.28
14	1.10	.24	.78	.27	1.00	.32

	Pereiopod V Isch L	Isch W	Bas L	Bas W	Cox L	Cox W
8	.22	.18	.80	.50	.26	.44
9	.26	.20	.91	.55	.30	.47
10	.30	.23	1.00	.60	.31	.51
11	.35	.26	1.20	.69	.40	.62
12	.38	.29	1.30	.76	.43	.68
13	.41	.29	1.30	.77	.45	.69
14	.43	.32	1.50	.86	.50	.77

APPENDIX B

Table B-1. Length to width relationships of various regions of the adult female Ampithoe valida Smith for seven different size classes.

Table B-2. Length to length relationships of various regions of the adult female Ampithoe valida Smith for seven different size classes.

Table B-3. Length to length relationships of various regions of the immature Ampithoe valida Smith for six different size classes.

Table B-1. Mean Length to Width Relationship

mm. Size Class	Eye	IAL	Md palp S_3	Mx palp S_2	Telson
8	1/.82	1/3.00	1/.35	1/.32	1/1.33
9	1/.72	1/2.90	1/.40	1/.33	1/1.34
10	1/.77	1/2.86	1/.34	1/.36	1/1.33
11	1/.72	1/2.92	1/.37	1/.34	1/1.36
12	1/.73	1/2.94	1/.38	1/.31	1/1.30
13	1/.80	1/3.26	1/.41	1/.34	1/1.27
14	1/.79	1/3.52	1/.41	1/.36	1/1.31
$\bar{\bar{X}}$	1/.76	1/3.06	1/.38	1/.34	1/1.32

	Gn I Pro	Gn I Car	Gn I Mer
8	1/.51	1/.64	1/.93
9	1/.50	1/.62	1/.87
10	1/.53	1/.62	1/.84
11	1/.51	1/.61	1/.89
12	1/.54	1/.61	1/.90
13	1/.52	1/.61	1/.91
14	1/.50	1/.57	1/.84
$\bar{\bar{X}}$	1/.61	1/.61	1/.88

Table B-1. Mean Length to Width Relationship

mm. Size Class	Gn II Pro	Gn II Car	Gn II Mer
8	1/.59	1/0.97	1/.72
9	1/.58	1/1.00	1/.70
10	1/.58	1/0.94	1/.68
11	1/.58	1/0.97	1/.75
12	1/.61	1/0.97	1/.72
13	1/.60	1/0.97	1/.68
14	1/.59	1/0.96	1/.66
$\bar{\bar{X}}$	1/.59	1/.97	1/.70

	Per I Pro	Per I Car	Per I Mer	Per I Cox
8	1/.27	1/.36	1/.63	1/.71
9	1/.25	1/.33	1/.53	1/.71
10	1/.30	1/.38	1/.57	1/.71
11	1/.28	1/.34	1/.53	1/.71
12	1/.25	1/.34	1/.52	1/.68
13	1/.26	1/.34	1/.52	1/.66
14	1/.23	1/.31	1/.50	1/.70
$\bar{\bar{X}}$	1/.26	1/.34	1/.54	1/.70

Table B-1. Mean Length to Width Relationship

mm. Size Class	Per II Pro	Per II Car	Per II Mer	Per II Cox
8	1/.27	1/.39	1/.65	1/.75
9	1/.25	1/.36	1/.56	1/.76
10	1/.28	1/.36	1/.60	1/.76
11	1/.28	1/.34	1/.58	1/.71
12	1/.27	1/.35	1/.57	1/.73
13	1/.27	1/.34	1/.55	1/.68
14	1/.25	1/.30	1/.51	1/.70
$\bar{\bar{X}}$	1/.27	1/.35	1/.57	1/.73

	Per III Pro	Per III Car	Per III Cox max min
8	1/.31	1/.61	1/1.10/.78
9	1/.31	1/.60	1/1.00/.78
10	1/.32	1/.58	1/1.00/.79
11	1/.33	1/.52	-1/1.00/.78
12	1/.33	1/.57	1/0.94/.81
13	1/.34	1/.53	1/0.94/.76
14	1/.32	1/.50	1/0.94/.77
$\bar{\bar{X}}$	1/.32	1/.50	1/0.99/.78

Table B-1. Mean Length to Width Relationship

mm. Size Class	Per IV Pro	Per IV Car	Per IV Cox
8	1/.25	1/.67	1/1.57
9	1/.24	1/.67	1/1.60
10	1/.25	1/.64	1/1.58
11	1/.24	1/.65	1/1.57
12	1/.23	1/.67	1/1.51
13	1/.26	1/.65	1/1.41
14	1/.24	1/.65	1/1.38
$\bar{\bar{X}}$	1/.24	1/.66	1/1.52

	Per V Pro	Per V Bas	Per V Cox
8	1/.23	1/.62	1/1.69
9	1/.23	1/.60	1/1.57
10	1/.23	1/.60	1/1.64
11	1/.23	1/.57	1/1.55
12	1/.23	1/.58	1/1.58
13	1/.23	1/.59	1/1.53
14	1/.21	1/.57	1/1.54
$\bar{\bar{X}}$	1/.23	1/.59	1/1.59

Table B-2. Mean Length to Length Relationship

mm. Size Class	Antenna I $P_1/P_2/P_3/FL$	Antenna II $P_4/P_5/FL$	Antenna II $P_4 + P_5/FL$
8	1/.85/.34/4.43	1/.92/2.00	1/1.04
9	1/.87/.38/4.92	1/.90/2.11	1/1.11
10	1/.92/.38/5.24	1/.92/1.82	1/0.95
11	1/.86/.34/5.40	1/.93/2.44	1/1.26
12	1/.94/.38/5.50	1/.95/2.60	1/1.33
13	1/.94/.38/4.88	1/.93/2.27	1/1.18
14	1/.90/.35/4.79	1/.90/2.64	1/1.39
$\bar{\bar{X}}$	1/.90/.36/5.02	1/.92/2.27	1/1.18

	Uropod I Ped/Ex/En	Uropod II Ped/Ex/En	Uropod III Ped/Ex/En
8	1/.54/.60	1/.63/.79	1/.43/.53
9	1/.57/.64	1/.63/.77	1/.46/.54
10	1/.54/.60	1/.60/.71	1/.41/.49
11	1/.56/.59	1/.64/.75	1/.41/.48
12	1/.60/.65	1/.64/.74	1/.45/.51
13	1/.59/.67	1/.64/.76	1/.42/.50
14	1/.63/.68	1/.65/.78	1/.41/.49
$\bar{\bar{X}}$	1/.58/.63	1/.63/.76	1/.43/.50

Table B-2. Mean Length to Length Relationship

mm. Size Class	Gn I Dac/Pal	Gn I Pro/Car/Mer
8	1/.93	1/.81/.52
9	1/.94	1/.80/.54
10	1/.94	1/.85/.53
11	1/.92	1/.84/.53
12	1/.93	1/.85/.55
13	1/.94	1/.87/.56
14	1/.91	1/.85/.53
$\bar{\bar{X}}$	1/.93	1/.84/.53

	Gn II Dac/Pal	Gn II Pro/Car/Mer
8	1/0.93	1/.59/.59
9	1/0.94	1/.57/.59
10	1/1.00	1/.60/.57
11	1/0.93	1/.57/.57
12	1/0.95	1/.62/.62
13	1/0.93	1/.60/.63
14	1/0.94	1/.62/.62
$\bar{\bar{X}}$	1/0.94	1/.59/.60

Table B-2. Mean Length to Length Relationship

mm. Size Class	Per I Pro/Car/Mer	Per II Pro/Car/Mer
8	1/.95/.89	1/.92/.89
9	1/.98/.98	1/.97/.95
10	1/.98/.98	1/.98/.95
11	1/.98/.94	1/ 1 /.94
12	1/ 1 / 1	1/.98/.96
13	1/.98/.98	1/ 1 /.98
14	1/.97/.98	1/ 1 / 1
$\bar{\bar{X}}$	1/.98/.96	1/.98/.95

	Per IV Pro/Car/Mer	Per V Pro/Car/Mer
8	1/.69/.86	1/.67/.84
9	1/.68/.85	1/.72/.91
10	1/.69/.89	1/.71/.92
11	1/.71/.92	1/.70/.94
12	1/.75/.99	1/.77/.98
13	1/.77/ 1	1/.74/.98
14	1/.71/.94	1/.71/.91
$\bar{\bar{X}}$	1/.71/.92	1/.72/.92

Table B-3. Mean Length to Length Relationship

mm. Size Class	Antenna I P1/P2/P3/FL	Antenna II P4/P5/FL
1	1/.80/.40/2.90	1/.66/1.80
2	1/.84/.46/3.70	1/.77/1.70
3	1/.80/.55/4.50	1/.83/1.60
4	1/.80/.44/4.50	1/.84/1.97
5	1/.87/.47/4.40	1/.88/2.10
6	1/.94/.44/5.00	1/.88/2.00

	Uropod I Ped/Ex/En	Uropod II Ped/Ex/En	Uropod III Ped/Ex/En
1	1/.63/.95	---------	----------
2	1/.50/.62	1/.31/.61	----------
3	1/.46/.53	1/.52/.74	1/.33/.66
4	1/.56/.65	1/.60/.80	1/.33/.58
5	1/.53/.63	1/.65/.72	1/.42/.58
6	1/.51/.60	1/.60/.75	1/.43/.65

APPENDIX C

Table C-1. Means of spination and setation counts taken on adult females of *Ampithoe valida* Smith for seven different size classes.

Table C-1. Mean Spination and Setation

mm. Size Class	Md Teeth	Mx I Teeth	Mx I Palp spn	Mx I Palp S_2 set	Mx II Inner Lobe *	Mx II Outer Lobe *
8	7	10	5.5	2.5	8.4	5.5
9	7	10	6.0	2.0	11.	6.0
10	7	10	6.0	2.8	10.8	5.0
11	7	10	6.1	2.5	14.6	7.5
12	7	10	7.1	2.4	14.4	7.7
13	7	10	7.6	3.2	14.8	7.0
14	7	10	7.6	3.0	18.6	10.0

* Refers to setae along the medial border to the dense apical tuft but does not include the apical tuft.

	Ant I articles	Ant II articles	Uro I Ped Lat	Uro I Ped Med	Uro I Ex Lat	Uro I Ex Med	Uro I En Lat	Uro I En Med
8	19.5	11.6	5.8	4.8	4.0	0	0	2.2
9	22.0	13.6	5.0	4.6	5.1	0	0	2.8
10	23.6	12.4	6.0	4.8	5.1	0	0	2.8
11	27.1	16.0	6.5	5.3	5.0	0	0	3.1
12	27.6	17.0	7.1	5.2	7.0	0	.14	3.2
13	25.0	15.5	6.0	5.4	5.4	0	0	3.2
14	25.0	18.0	7.0	5.0	7.6	0	0	4.6

Table C-1. Mean Spination and Setation

mm. Size Class	Uro II Ped Lat spn	Uro II Ped Med spn	Uro II Ex Lat spn	Uro II Ex Med spn	Uro II En Lat spn	Uro II En Med spn
8	2.8	2.0	2.6	0	0	2.0
9	2.7	2.9	3.0	0	.14	2.7
10	3.1	3.0	3.0	0	0	2.4
11	3.1	3.0	3.3	0	.33	3.0
12	3.2	3.0	3.7	0	.43	3.0
13	3.2	3.0	3.4	0	.30*	3.0
14	3.4	3.2	4.6	0	.20*	3.4

* Some individuals may have two spines present (Figure III-5, b).

	Uro III Ped Lat spn	Uro III Ped Post spn	Uro III Ped Med spn
8	1.0	2.6	1
9	1.0	2.6	1
10	1.0	3.2	1
11	1.1	3.1	1
12	1.0	3.0	1
13	1.2	3.4	1
14	1.0	3.6	1